MONOGRAPHS ON EXPERIMENTAL BIOLOGY

EDITED BY
JACQUES LOEB, Rockefeller Institute
T. H. MORGAN, Columbia University
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THE ELEMENTARY NERVOUS SYSTEM

BY

G. H. PARKER, Sc.D.

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PUBLISHED

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THE ELEMENTARY NERVOUS SYSTEM

BY

G. H. PARKER, Sc.D.

PROFESSOR OF ZOÖLOGY, HARVARD UNIVERSITY

53 ILLUSTRATIONS

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EDITORS' ANNOUNCEMENT

THE rapidly increasing specialization makes it impossible for one author to cover satisfactorily the whole field of modern Biology. This situation, which exists in all the sciences, has induced English authors to issue series of monographs in Biochemistry, Physiology, and Physics. A number of American biologists have decided to provide the same opportunity for the study of Experimental Biology.

Biology, which not long ago was purely descriptive and speculative, has begun to adopt the methods of the exact sciences, recognizing that for permanent progress not only experiments are required but that the experiments should be of a quantitative character. It will be the purpose of this series of monographs to emphasize and further as much as possible this development of Biology.

Experimental Biology and General Physiology are one and the same science, by method as well as by contents, since both aim at explaining life from the physico-chemical constitution of living matter. The series of monographs on Experimental Biology will therefore include the field of traditional General Physiology.

JACQUES LOEB,
T. H. MORGAN,
W. J. V. OSTERHOUT.

AUTHOR'S PREFACE

The dependence of human affairs upon the nervous system of man is so absolute that it was inevitable, as soon as this relation was understood, that the activities of the simpler animals should be interpreted as though these creatures were miniature human beings. That such interpretation was carried far beyond its legitimate bounds, even by the scientifically trained, is now admitted on almost all sides, but it is no easy or simple task to ascribe to this movement its proper bounds. That these bounds are vastly more restricted than has usually been supposed is certain. An approach to a clearer understanding of what they are is assured through the application of experimental and quantitative methods to the questions concerned rather than by a continuation of the older more purely observational procedure. It is from this standpoint that an attempt has been made in this volume to portray the elementary nervous system as it exists in the simpler animals and in the simpler parts of the more complex forms. It is believed that this treatment of the subject may help in the solution of the general problem by removing once and for all some of the old misunderstandings concerning the nervous system and by inviting the student's attention to new methods of attack.

The subject matter of the volume is drawn almost entirely from the three simpler phyla of the multicellular animals, the sponges, the cœlenterates, and the ctenophores. This is intentionally done for the reason that the activities of such animals as the echinoderms, worms and

so forth, will be treated in another monograph of this series, one by Dr. A. R. Moore. It is also to be remarked that in Chapter XIII of the present volume, which deals with the hydroids, the account of the activities of these animals is rather more detailed than that accorded to other forms. This method of treatment has been followed in consequence of the fact that the details of the responses of hydroids are by no means so readily available in the literature as are those of other groups of cœlenterates.

The writer is indebted to his wife for a full revision of the manuscript and to the editors of the series for many helpful suggestions. He is also under obligations to Mrs. Donald E. Woodbridge for the preparation of the illustrations.

G. H. P.

Harvard University, Cambridge, Mass.
November, 1918.

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CHAPTER I

INTRODUCTION

The elementary nervous system is that type of nervous system in which the structural and functional elements present themselves in their simplest states. It is most extensively represented in the lower multicellular animals, but it is found locally in as highly differentiated forms as the vertebrates. It probably represents the primitive nervous system in that it reproduces much that must have been characteristic of nervous organs in their earliest stages of evolution. It has been an object of investigation and interest only within comparatively recent years. Its derivative, that complex aggregate of organs known as the central nervous system of the higher animals, attracted the attention of anatomists and physiologists at a much earlier period. This was doubtless due to the unusual development of the central nervous organs in man and other higher animals. The human brain is a structure whose size and position naturally compels attention, whereas the chief nervous organs in many of the lower animals are often so insignificant as to be easily overlooked.

Although the first attempts at elucidating the structure and functions of the nervous system were made on

the higher animals, it was a long time before this system was recognized as the exclusive seat of the most striking characteristic of man, his mental life. Only gradually was it discovered that his conscious states represent the action of a single system of organs, the nervous system, as contrasted with the rest of his body.

To the ancients this conscious life, whose chief attribute is personality, seemed to permeate the whole human frame. In fact, Aristotle, who was such an accurate observer and profound thinker in so many fields of biology, denied positively that the brain was in any direct way concerned with sensation and declared the heart to be the sensorium commune for the whole body. To Galen is ascribed the belief that the brain is the seat of the rational soul, the heart the location of courage and fear, and the liver that of love. The distribution of the elements of personality over the physical body finds its expression in the common speech of to-day, particularly in relation to the heart, which is widely accepted by the popular mind as the seat of the more tender emotions. Although this opinion may commonly imply a certain amount of poetic license, it is quite certain that many an untrained person holds even at the present time to a literal interpretation of the ancient view of the location of sensations. The pain of a pin prick is commonly believed by many persons to be where the pin enters the skin. To them nothing seems more obvious and certain than that the punctured spot is the seat of the pain, and any attempt to change their views on this point will usually be regarded by them with suspicion and mistrust, for it seems contrary to common sense.

Nevertheless, it is well known that if a nerve distributed to a given area of skin is cut at some distance from

that area, the spot, though unaffected by the operation in any direct way, will give rise to no further sensations even when it is severely injured. Hence, it is clear that the pain does not reside simply in the skin. But not only may pain thus be absent from a given area of skin; it may be present when the skin with which it is supposed to be associated is absent. Persons who by accident or otherwise have lost an arm or a leg often experience long after the loss vivid and intense sensations from definite parts of the missing member. So precise and sharp are these sensations and so certainly do they seem to be associated with the lost part that some of the less knowing of these unfortunates have attempted to exhume or otherwise get possession of the lost member in an endeavor to alleviate their unpleasant sensations.

These misunderstandings, for such they are, can be swept away at once and the matter put in its true light when we recognize that our sensations are not located in the peripheral parts affected, but in the central nervous system, and within that portion of it known as the cerebral cortex. As long as this organ is intact, sensations may arise, and, though these are usually due to nervous impulses from the sensory surfaces, they may be called forth by an internal stimulus as well. Thus it is that a missing arm may be represented by sensations years after it has been severed from the body. With a loss of an appropriate part of the cerebral cortex, however, comes a loss of sensation that is absolute and final. From this there is no recovery (Parker, 1916 *b*).

This modern view of the relation of sensation to the nervous system was initiated by the anatomists and physiologists of the Renaissance. Thus, Vesalius taught, in the sixteenth century, that the chief soul was engen-

dered in the brain by virtue of the powers of the proper material and form of that organ. And, although Stahl attempted, a century and a half later, to revive the belief that the soul and the sensorium commune were diffused over the whole body, that is, were resident as well in the tip of the finger as in the brain, the idea of the localization of these active properties in the nervous system became so well grounded through the investigations of the physicians of that time, particularly Haller, as to assume the form of permanency. This growth of knowledge led directly to the modern view that personality is, strictly speaking, a property of the nervous system and is in no true sense the direct result of any other system of organs. (Foster, 1901.)

The nervous system, to be sure, is embedded among the other organs of the body, and the environment thus provided influences profoundly its condition and action; but what is meant by individual personality, acuteness or dulness of sense, quickness or slowness of action, temperamental traits, such as a gloomy or bright disposition, incapacity, shiftlessness, honesty, thriftiness, or sweetness, are all in the strictest sense functions of the nervous system. Hence, it is a matter of no small biological interest to ascertain from the conditions presented in the simpler animals which of these various states are elemental and what has been the probable line of evolution of that system of organs with which our personality is so indissolubly connected (Parker, 1914 *a*).

The nervous system of the higher animals, though enormously complex in its organization, is composed of relatively simple cellular elements, the neurones, arranged upon a comparatively uniform plan. This plan is well exemplified in the spinal nerves and spinal cord of the

vertebrates (Fig. 1). In this complex the sensory neurones, whose cell-bodies lie in the dorsal ganglia, extend from the integument through the dorsal roots to the gray matter of the cord. Motor neurones, whose cell-bodies are situated within the gray matter of the cord, reach from this region to the muscle-fibers which they control. These two classes of neurones would seem to be sufficient for all ordinary reflex operations, but the cord contains within its limits other neurones which serve to connect

FIG. 1.—Diagram of the primary sensory *s* and motor *m* neurones of the spinal cord of a vertebrate showing their connections with the integument *i* and with muscle fibers *mf*.

one part of its structure with another. These neurones, which have been called internuncial neurones, are interpolated between the sensory and motor elements just described and must thereby lengthen and extend the courses of the reflex impulses. Such neurones make up a large part of the substance of the cord and doubtless increase enormously its internal connections. In the brain they not only add to the nervous interrelations, but they afford in the region of the cerebral cortex the material basis for all intellectual operations.

The plan of neuronic arrangement as exemplified in the vertebrates also obtains in animals as lowly organized as the earthworm (Fig. 2). In this form the sensory

neurones, whose cell-bodies are situated in the integument instead of being gathered into special ganglia, extend, as in the vertebrates, from the skin to the central nervous organs, the brain or the ventral ganglionic chain. The motor neurones are essentially duplicates of those in the vertebrates in that their cell-bodies lie within the central organ whence their fibers extend to the appropriate

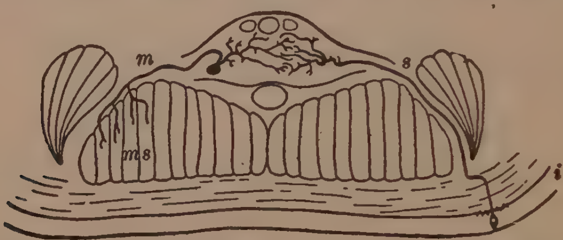


FIG. 2.—Diagram of the primary sensory *s* and motor *m* neurones of the ventral ganglionic chain of the earthworm showing their connections with the integument *i* and with the muscles *ms*. (Modified from Retzius.)

musculature. Internuncial neurones are also abundantly present in the earthworm, though their function here, in contrast with that in the higher vertebrates, is pure nervous intercommunication, for it is very unlikely that the earthworm possesses what in any strict sense of the word can be called intelligence. Thus from a morphological standpoint, the nervous systems of the higher animals, even including such forms as the earthworm, have much in common, their three sets of interrelated neurones, sensory, motor, and internuncial, being arranged upon what is in the main a uniform plan.

Considered from a physiological standpoint, the nervous system with its appended parts as just sketched falls in the higher animals into three well-marked categories. On the exterior of these animals are to be found sense organs or receptors such as the free-nerve terminations

of the sensory neurones in the vertebrates or the sensory cells in the integument of the earthworm. These organs have for their function the reception of the external stimuli and the production of the sensory impulses. The receptors are connected by nerve-fibers with the central nervous organ or adjustor composed of the central ends of the sensory and the motor neurones and of the internuncial neurones. Here the impulses arriving from the receptors are directed toward the appropriate groups of muscles by which the animal may respond to the stimulus and, if the animal is highly organized, impressions are made upon the adjustor which, as memories, may become more or less permanent parts of the animal's nervous equipment. Finally the adjustors are connected by nerve-fibers with the third set of elements, the effectors, which as muscles, electric organs, glands, etc., enable the animal to react on the environment. Thus three physiological categories are to be distinguished which in the order of their sequence in action are sense organs or receptors, central nervous organs or adjustors, and muscles or other effectors.

It is to be noted in passing, that the physiological scheme just outlined includes a wider range of parts than is generally admitted under the head of the nervous system. The additional parts are the effectors, which, as will be shown later, form as truly a part of the whole system as do the sense organs or the central nervous organs. Since the term nervous system does not ordinarily include the effectors, it is perhaps best to designate the whole chain of related parts, receptors, adjustors, and effectors, as the neuromuscular mechanism, and in dealing with the elementary nervous system it will be found important to keep this relation in mind, for in such an inquiry, the

real question that must be confronted concerns the interrelations within the neuromuscular mechanism rather than those that are simply within the nervous system itself.

The type of neuromuscular mechanism described in the preceding paragraphs in which a group of receptors is connected with a well centralized adjustor that in turn controls a complex system of effectors, is found only in the more differentiated animals. Certainly in the simple forms, like the jellyfishes, corals, sea-anemones and so forth, only the slightest evidence of this type of nervous organization can be discovered. Nevertheless, these animals possess a neuromuscular mechanism, but on so simple a plan that investigators have long been inclined to regard it as representing the first step in the differentiation of neuromuscular organs. This plan of structure is well represented in the sea-anemones. Each of the two layers of cells that make up the living substance of the sea-anemone's body consists ordinarily of three sublayers; a superficial or epithelial layer, a middle or nervous layer, and a deep or muscular layer (Fig. 3). The epithelial layer contains, besides many other kinds of cells, large numbers of sensory cells which terminate peripherally in bristle-like receptive ends and centrally in fine nervous branches. These fine branches constitute collectively the middle or nervous layer in which occasionally large branching cells, the so-called ganglionic cells, occur. Immediately under the nervous layer is the deep layer of elongated muscle-cells.

FIG. 3.—Ectodermic layer from the tentacle of a sea-anemone showing the three sublayers, epithelial *e*, nervous *n*, and muscular *m*.

The condition thus briefly described is present over much of the sea-anemone's body, and though the nervous layer may be somewhat emphasized in some regions, it cannot be said to be really centralized in any part. Hence this type of nervous system has been designated as diffuse in contrast with the centralized type found in the higher animals.

What is really present in the neuromuscular portion of the sea-anemone's body is a large number of peripheral sensory cells whose deep branching ends connect more or less directly with the muscles, that is, without the intervention of a true central organ. This neuromuscular system, if described in the terms already used, could be said to be composed of receptors and effectors without an adjustor or at least with this member present in only a most undeveloped state. Hence the adjustor or central organ is in all probability an acquisition that represents a later stage in the evolution of the neuromuscular mechanism than that seen in the cœlenterates.

If the cœlenterates represent a stage in the development of the neuromuscular mechanism in which sensory cells and muscles are the only important parts present, it is natural to ask if there is not a still more primitive state from which the cœlenterate condition has arisen. On this question several hypotheses have already been advanced. Claus (1878) and, subsequently, Chun (1880) maintained that originally the nervous system and the muscles were differentiated independently and that they became associated only secondarily. This view has deservedly received very little attention, for it is extremely difficult to conceive of an animal that would develop receptive ability without at the same time acquiring the power to react. Such an animal would have a certain

resemblance to a person suffering from complete motor paralysis who might still be able to receive impressions from the exterior and even to reflect on them, and yet would be incapable, in consequence of the complete separation of nerve and muscle, of carrying out activities that would maintain a harmonious adjustment with the exterior. Not only does this view of the independent origin of nerve and muscle meet with the inherent and serious difficulty just alluded to, but among the lower forms not a single animal is known in which nerve is unassociated with muscle. Hence the hypothesis of Claus and of Chun has received very little serious consideration.

Much less subject to criticism than the hypothesis of the independent origin of nerve and muscle is Kleinenberg's theory of the neuromuscular cell. In 1872 Kleinenberg announced the discovery in the fresh-water hydra of what he designated as neuromuscular cells. The peripheral ends of these cells were situated on the exposed surface of the epithelium, of which they were a part and were believed to act as nervous receptors; the deep ends were drawn out into muscular processes and served as effectors to which transmission was supposed to be accomplished through the bodies of the cells. Each such cell was regarded as a complete and independent neuromuscular mechanism, and the movements of an animal provided with these cells was believed to depend upon the simultaneous stimulation of many such elements. It was Kleinenberg's opinion that these neuromuscular cells divided and thus gave rise to the nerve-cells and muscle-cells of the higher animals. In fact, he declared that the nervous and muscular systems of these animals were thus to be traced back to the single type of cell, the neuromuscular cell, which morphologically and physiologically rep-

resented the beginnings of both. But Kleinenberg's neuromuscular cells were subsequently shown by the Hertwigs to be merely epitheliomuscular cells and no intermediate stage between them and the differentiated neuromuscular mechanism of higher forms was ever discovered. Hence this hypothesis, too, has been largely abandoned (Parker, 1911).

Some years later, in 1878, the Hertwigs published an account of the neuromuscular mechanism in cœlenterates. In this account they described the sensory cells, the ganglionic cells, and the muscular cells of the cœlenterates, and maintained that these elements arose not by the division of single cells, as stated by Kleinenberg, but that each element was differentiated from a separate epithelial cell and yet in such a way that during differentiation all these elements were physiologically interdependent. This hypothesis of the simultaneous differentiation of nerve and muscle, which has been the current opinion among biologists for more than a generation, is not without its serious difficulties, for it appears that in the sponges, which are more primitive animals than the cœlenterates, there are muscles of a very simple type but without any associated nerve (Parker, 1910 *a*). In fact, no nervous tissue of any kind has been definitely identified in sponges. It, therefore, appears that of the two elements, nerve and muscle, the latter may exist independently of the former and in such a way as to indicate its more primitive character. From this standpoint it seems that the receptor-effector system of the cœlenterates was preceded by a simpler state in which only the effector element, muscle, was present and that this element may, therefore, be regarded as the original one in the evolution of the neuromuscular mechanism. Muscle once

developed as an effector gave occasion for the addition of receptors or sensory elements after which the adjustor or central nervous mechanism was differentiated. Hence in dealing with the elementary nervous system it will not be inappropriate to consider first such independent effectors as are found in sponges after which the receptor-effector system of the cœlenterates may be dealt with, in part as a system in itself and in part as the source of the differentiated receptor-adjustor-effector systems of the more complex invertebrates and the vertebrates. Heretofore the approach to this subject has been chiefly from the side of anatomy and histology; but important as this line of research has been, the more recent experimental results have shown that the physiological side of the question is quite as illuminating as the morphological. In the following pages some of the more important problems of the elementary nervous system will be discussed. While these problems will be taken up chiefly from a functional standpoint, the structural aspect of the questions concerned will not be omitted, for in discussions of this kind the double viewpoint is more likely to lead to sound conclusions than if only one aspect is kept in sight (Parker, 1909, 1910 *b*, 1914 *b*).

SECTION I. EFFECTOR SYSTEMS

CHAPTER II

SPONGES

Sponges are such inert organisms that their membership in the animal series was for a long time unsuspected. Their methods of development, however, settled this question beyond dispute. In form they are either single, more or less goblet-shaped animals (Fig. 4) or somewhat amorphous colonies whose chief activity is exhibited in the very considerable currents that they produce in the surrounding water. These currents enter the substance of the sponge through innumerable pores scattered over the surface of its body, pass through its more solid parts by a system of canals that converge on a central cavity, the cloaca, from which they emerge by a large opening, the osculum. This opening is situated at the apex of the individual sponge or, in the case of a colony, each osculum is ordinarily on a somewhat conical elevation rising above the general surface of the colony.

The currents that emerge from sponges are often so considerable as to deform the surface of the water above them much as is done by a vigorous spring. They are produced by the action of the choanocytes or flagellated cells that line the canals in the body of the sponge or that invest more specialized chambers interpolated on the course of these canals. So far as can be judged by the examination of the inner parts of sponges, the choanocytes are incessantly active, and the obliteration and revival of currents as seen in many of these animals are

due not to changes in the activity of the choanocytes but to other causes.

Some sponges, such as the fingered form *Stylotella,* appear, when out of water, to be more or less shrivelled or contracted and under other circumstances to be plump and well rounded-out. The differences, which, for reasons to be mentioned presently, are known not to be due to the simple physical loss of fluid, are apparently dependent upon a general contractility of the whole flesh of the sponge which, though slight, may nevertheless enable the sponge to change its form somewhat. Aristotle in the fourteenth chapter of his fifth book on the history of animals makes the interesting statement that the sponge is supposed to possess sensation because it contracts if it perceives any movement to tear it up and it does the same when the winds and waves are so violent that they might loosen it from its attachment. He further adds in his characteristic way that the natives of Torona dispute this.

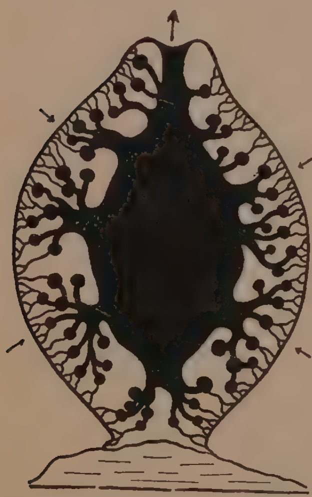


Fig. 4.—Diagram of the canal system of a calcareous sponge (modified Haeckel). The innumerable superficial pores receive water from the exterior, as shown by the arrows on the sides; the osculum at the apex discharges water to the exterior.

The idea that the common flesh of the sponge is contractile is not without modern support. Merejkowsky (1878) stated that if the sponge *Suberites* is so placed that it is partly out of water, it will curve the body until it is under water as much as possible, and if the body is then

covered with water, it will return to its former position.

It must be evident, from what has already been stated, that much of the common flesh of *Stylotella* is contractile. As already noted, specimens out of water quickly assume a shrivelled and rugose appearance as though the flesh had contracted on a resistant skeleton, a condition that it also quickly assumes in quiet seawater. Moreover, if a sponge is placed partly in running seawater and partly in the air, the portion in the seawater remains smooth and that in the air becomes rugose. Specimens made rugose either in the air or in quiet water soon recover their smooth appearance on being placed in running seawater. Air or quiet water may then cause a contraction of the common flesh of *Stylotella,* a condition counteracted by running water.

The contraction of the common flesh can also be well seen around some of the larger cavities, such as the cloacal cavity. If a long finger of *Stylotella,* whose two ends have been cut off and whose cloacal cavity extends along one of its sides, is placed in quiet seawater, the cloacal cavity is soon indicated by an external groove due apparently to the partial collapse of the cavity. This groove, however, is caused not by collapse, but by the contraction of the common flesh which as partial partitions or even trabeculæ is abundant about the sides of the cloaca. On returning the finger to running water the flesh relaxes and the groove mostly disappears.

Although the common flesh of *Stylotella* is unquestionably contractile, the body of this sponge has never been observed to move as a whole in consequence of this contractility. Thus in no instance did a finger of *Stylotella* when partly immersed in seawater, bend farther into the water, though fingers have been allowed to stand in

positions favorable for this form of response for over a day. Nor have fingers been observed to turn in conformity to the direction of the general current of water in which the sponge was standing. In some instances the fingers of *Stylotella* are not directed straight upward, but their tips are turned to one side or the other so that their oscula open laterally. A number of these sponges were set, some with their oscula facing the general current, others with these openings away from the current, and still others sidewise to the current. After three days none of these had noticeably changed their directions, thus giving no evidence of a general movement of the body.

Attempts were also made to get evidence of the general movement of *Stylotella* through geotropic stimulation. This sponge ordinarily grows with its fingers and oscula directed upward, as though it were negatively geotropic. A large colony was, therefore, kept inverted in an aquarium of circulating seawater for about a week on the assumption that the fingers might be brought to turn from this unusual position, but at the end of this period there was no discoverable change of position. This observation, however, does not prove that *Stylotella* is not geotropic. Slight evidence of its geotropism is to be found in its method of regenerating oscula. When a moderately long finger of *Stylotella* is cut off and the whole of its oscular end removed, the cylindrical body thus resulting will under favorable conditions form a new osculum. Whether this regeneration will take place at the end nearer or farther from the former osculum seems to depend chiefly on the position of the piece of sponge with reference to gravity. If the end that was nearer the former osculum is uppermost, it always regenerates

a new osculum; if it is down, the opposite end very generally regenerates the new organ. Thus in the regeneration of the osculum, *Stylotella* shows some slight geotropic activity, and while it must be admitted that the common flesh of this sponge is contractile, this contractility does not seem to result in movements of the body as a whole such as might be looked for in geotropic and other like responses. It is possible that in this sponge the skeleton, which is well developed, is too resistant to allow the body as a whole to be bent, and that, therefore, the contractility of the common flesh can make itself manifest only in the local ways already mentioned.

But, as has already been intimated, the chief activity of sponges is not shown in the general movements of their bodies, but in the currents of water that they produce. These currents are due to the incessant activity of the choanocytes in the passages within the body of the sponge. Access to these passages is gained through the innumerable pores on the general external surface of the sponge and the exit from them is through the cloaca and the relatively large terminal opening of the cloaca, the osculum. The cessation or revival of these currents, as seen in many sponges, is not due to changes in the activity of the choanocytes but is dependent upon the closing or opening of the pores and of the osculum, whereby the water current is checked or allowed to pass.

The pores on the surface of *Stylotella* are of the kind designated as dermal pores, or ostia, in that instead of leading directly to the inlet canals of the flagellated system they admit to relatively large subdermal spaces which in turn communicate through the incurrent canals proper with the flagellated chambers (Fig. 5). These chambers empty through the excurrent canals into the cloaca.

The opening and closing of the dermal pores in *Stylotella* has been observed directly in living preparations by Wilson (1910), whose account will be referred to presently. In the following experimental tests the presence or absence of currents was used as an indication of the state of the pores. The demonstration of these currents has been accomplished from the earliest times by the ad-

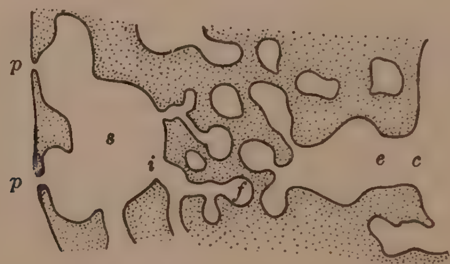


FIG. 5.—Radial portion of a transverse section of *Stylotella;* the flesh of the sponge is dotted, the cavities are undotted; on the extreme left is the dermal membrane pierced by two pores *p* that lead into a large subdermal space *s*, from which incurrent canals *i* lead to the flagellated chambers *f*, which in turn open by excurrent canals *e* into the cloaca *c*.

dition to the water of some such substances as carmine, starch, or indigo, whose particles could then be followed as they were carried in the moving water. Latterly this method has been severely criticized by von Lendenfeld (1889), who claims that even these small suspended particles mechanically stimulate the sponge and cause it to close its pores. Von Lendenfeld used milk as an indicator and found no objection to it. With *Stylotella* it is easy to demonstrate the pore currents with carmine and the like, and, so far as could be discerned, this material could be used without causing partial closure of these apertures. In fact, as stated by Bidder (1896), carmine particles seemed to have no effect whatever on the dermal pores, but were swept into the interior of the sponge with

great freedom for hours at a time. It must, however, be confessed that not only carmine but even milk is an unnatural substance for a sponge, and as *Stylotella* lives in water that ordinarily contains much fine suspended material, it was found necessary only to watch this material to gain all the information that was needed as to the direction or strength of the currents at the pores.

In testing the pores, a finger of sponge was pinned under the microscope in a small glass aquarium so arranged that a continuous current of seawater could be kept running through it, and by watching the suspended particles along the sides of such a preparation under a magnification of about ninety diameters, it was comparatively easy to ascertain whether the pore currents were running or not. As a rule the objective of the microscope was necessarily plunged under the surface of the seawater. In making observations it was, however, necessary for the time being to stop the current of seawater that was running through the small reservoir in which the sponge was, otherwise the movement of the suspended particles over the surface of the sponge was so rapid that it was impossible to tell whether they entered a pore or simply glided past it. When this current was shut off, the osculum often closed and under such circumstances, as might have been expected, the pore currents ceased. To be certain that the cessation of these currents was due to the closure of the outlet, the tip of the sponge finger including the closed osculum was cut off with the result that the pore currents almost immediately began again. Moreover, when the cut oscular end of a finger on which pore currents could be easily seen was ligated, these currents ceased at once and on the removal of the

ligature they at once recommenced. From these observations it is quite clear that the osculum controls in a purely mechanical way the current within the sponge. When the osculum is open, this current may run; when it is closed, the current ceases even though the dermal pores are open and the choanocytes continue to beat. In view of these facts the oscular ends of the fingers of *Stylotella* were regularly removed.

Although the presence of a pore current is conclusive evidence of the open condition of the pores, its absence

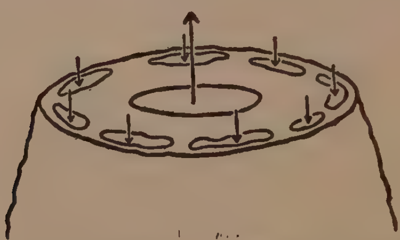


Fig. 6.—Diagram of a finger of *Stylotella* from which the tip has been cut showing currents entering the subdermal spaces and emerging from the cloaca.

is not proof that the pores are closed even supposing that the oscular end is cut off, for it is conceivable that the choanocytes may cease to beat, in which case the cessation of the currents would be misleading as to the condition of the pores. To meet this difficulty a simple procedure was adopted. If the oscular end of a finger of *Stylotella* is cut off at some distance from the osculum itself, the cut face includes not only the cloaca and some of the flagellated chambers, but also the subdermal spaces (Fig. 6). An examination of the currents from such a cut end will show a large, slow, central current emerging from the cloaca, and a considerable number of smaller more rapid currents entering the surrounding subdermal

cavities. These cavities form a set of intercommunicating spaces over the whole surface of the sponge, and the currents that set into them at the cut end depend largely upon the action of the choanocytes. If, now, no inward currents can be detected at the dermal pores but currents can still be seen to enter the subdermal cavities at their cut ends, it is clear that the absence of the currents at the pore entrances is due to the closure of the pores, and not to the cessation of the choanocytes. In this way the entrance of currents into the dermal pores can be used to indicate the open condition of the pores, and their absence, when coupled with currents into the subdermal spaces, to indicate the closed condition of the pores.

The means of inducing the opening and closing of the dermal pores in *Stylotella* as tested on preparations such as those described in the last paragraph were found to be numerous. The pores closed on injury inflicted in the neighborhood of the surface under inspection. They also closed when the seawater passing through them contained a small amount of ether (1/200), chloroform (1/200), strychnine (1/15,000), or cocaine (1/1000). They were apparently unaffected by mechanical stimulation, except injury, by temperatures as low as 9 degrees centigrade and by light. They opened in solution of atropin (1/1000), of weak cocaine (1/10,000), in dilute seawater, deoxygenated seawater, and warm seawater, 35 degrees centigrade (Parker, 1910 *a*).

The mechanism of opening and closing the dermal pores is more complex than has generally been assumed and has been very adequately described by Wilson (1910). In *Stylotella,* according to this author, the membrane covering each subdermal cavity and containing the pores,

the so-called dermal membrane (Fig. 7), is composed of an external epidermis which is believed to be syncytical and not cellular as heretofore assumed, of an intermediate mesenchyme containing spicules, and of an inner epithelioid membrane forming the lining of the subdermal cavity. Each pore consists of two parts, the pore or actual opening at the surface and the pore canal, a

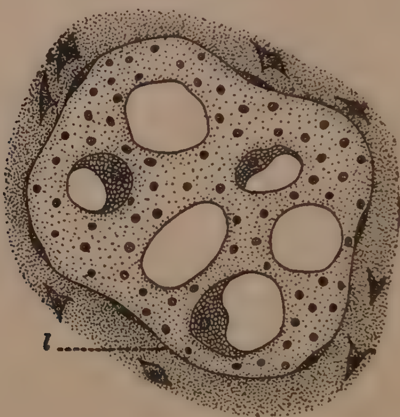


FIG. 7.—Dermal membrane over a subdermal cavity in the sponge *Stylotella* seen from the exterior as a somewhat transparent preparation. The outline of the subdermal cavity is indicated by the line of limiting cells *l*, within which is the dermal membrane pierced by six pores, three of which are partly closed by pore membranes. (After Wilson, 1910.)

very short canal that leads through the thickness of the dermal membrane to the subdermal cavity below. In *Stylotella* the pores can be seen to contract and to close by the activity of the epidermal syncytium (Fig. 8). With the closure of the pore this layer forms over the external end of the pore canal an extremely thin sheet, the pore membrane, near the middle of which the pore has disappeared. In this state the pore membrane is somewhat like the head of a drum, the pore canal representing the body of the drum. In other sponges studied by Wil-

son, *Reniera* and *Lissodendoryx,* not only may the pores close by the formation of a pore membrane, but this process may be supplemented by a closure of the pore canal itself. This is probably due, according to Wilson, to a contraction of the epithelial lining in the pore canal acting after the fashion of a sphincter. Thus there appear to be two somewhat independent devices for the closure of the pores, the pore membrane and the pore

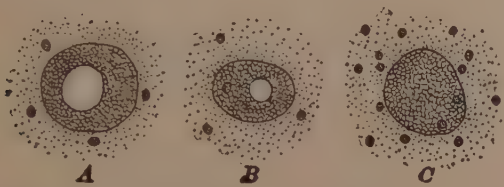


FIG. 8.—Three dermal pores in *Stylotella* showing steps in their closure by the pore membrane; *A*, partly closed; *B*, more nearly closed; *C*, completely closed. (Modified from Wilson, 1910.)

canal sphincter. All three sponges studied by Wilson were found to close their pores by means of pore membranes. Contraction of the pore canals was observed in *Reniera* and in *Lissodendoryx,* but not in *Stylotella,* though this sponge was not so favorable for such observations.

The closure of the pore canals, according to Wilson, is quite obviously dependent upon the sphincter-like band of cells on the wall of the canal. These cells are in every way comparable to a primitive form of smooth muscle-fiber. Their superficial position places them in contact with the water passing through the canal and, as they respond to the differences in this water, they are without doubt capable of direct stimulation. The pore membrane is less muscle-like in its action than the wall of the pore canal is and yet its movement is hardly to be described as

purely amœboid. It seems to represent a stage of differentiation between amœboid motion and simple muscle contraction which may well indicate the kind of contractility that the common flesh of the sponge possesses. But wherever these two types of tissue belong, they certainly both exhibit nothing in their activities that suggest a coördinating system. They act with great independence and as though they were stimulated directly, and in this respect they exhibit all the characteristics of independent effectors.

CHAPTER III

SPONGES (*Continued*)

The oscula of sponges are, in comparison with their pores, relatively large openings and hence they admit of experimental treatment such as is not possible with the pores. In *Stylotella* each finger ordinarily carries at its free end a single large osculum. The opening and closing of this osculum is the most obvious response of this sponge. If a colony under ordinary conditions is examined, some of the oscula will almost certainly be found closed, though the majority will be widely open. If a small colony is closely inspected under a low power of the microscope, the open oscula will be seen to emit a large number of minute particles indicating that a current is setting out through these openings. In what seem to be closed oscula a minute but otherwise similar current can often be detected, showing that they are really not closed. Some oscula, however, show absolutely no current, though it has been invariably found that when in such cases the oscular tip is cut off, the current can be seen almost instantly and it is, therefore, concluded that at times the oscula do close completely and thus check absolutely the current that ordinarily passes through them.

In order to get some idea of the natural movements of the oscula, a vigorous colony of *Stylotella* was isolated and three of its oscula were kept under approximately hourly observation for three days. The results of these observations are summarized in Table 1.

TABLE 1

Periods of Time in Hours and Minutes During which in the Course of Three Days Oscula 1, 2 and 3 were Open or Closed

Number of the Osculum	Time in hours and minutes of each successive period of open or closed state								Total time in 72 hours	
	Open	Closed	Open	Closed	Open	Closed	Open	Closed	Open	Closed
Osculum 1.....	0.45	2.00	19.05	3.20	20.15	7.50	2.35	16.10	42.40	29.20
Osculum 2.....	21.50	3.20	24.20	1.30	21.00	....	....	....	67.10	4.50
Osculum 3.....	0.45	0.25	21.40	2.35	23.50	0.15	23.10	....	68.45	3.15

Since the three oscula whose conditions are recorded in Table 1 were on the same colony and near together and were exposed to almost identical surroundings, the fact that osculum 1 was closed on the average one hour in every two and a half, while oscula 2 and 3 were closed only one hour in every eighteen, must be attributed to the difference in constitution of osculum 1 as contrasted with that of the other two. The condition of general openness as exemplified by oscula 2 and 3 is doubtless typical for these organs. At least in any vigorous sponge under normal conditions, the majority of the oscula will be found open much of the time.

The closure of the oscula can be brought about in a variety of ways. When a colony of *Stylotella* is transferred from running water in the exterior to a collecting bucket of quiet water, the oscula commonly close. They reopen on being brought again into running water. This and many other similar experiments pointed to the importance of currents in keeping the oscula open, but this form of experiment did not show what particular aspect of the current caused the osculum to open or to remain open. Did the sponge give out excretions that in quiet water gathered to such an extent in its immediate neighborhood as to cause its oscula to close and only on the

removal of these by a current of water would the oscula open, or did the current carry oxygen to the sponge or act in a purely mechanical way to induce the opening of the oscula? To test these matters the following simple experiment was tried. Three cylindrical glass aquaria of considerable size were placed at three levels so that the water from the uppermost aquarium could be siphoned freely into the intermediate one, from which the water overflowed into the third. Having filled the apparatus with seawater, it was possible to keep it running continuously with the *same* seawater by returning that which collected in the third or lowest aquarium to the uppermost one. If, now, the current of seawater carried away excretions from the sponge or brought oxygen to it and these operations had anything to do with the opening of the oscula, the use of the same water over and over again ought soon to bring on a condition that would no longer cause the oscula to open. But sponges placed in the current of the middle aquarium remained with their oscula open for hours in seawater that had been used many times over. Moreover, the oscula closed quickly when the current was cut off and reopened soon after it was started again. It, therefore, appears that the mechanical stimulation of a current of water is an effective means of opening or keeping open the oscula of *Stylotella*.

These first experiments were made on whole colonies of *Stylotella* and only the general condition of the oscula was recorded. It was desirable, however, to ascertain what part of the sponge must be exposed to the current to induce an opening of the osculum or the reverse. To test this question a colony of *Stylotella* was placed in a strong current of seawater and, when the oscula were well opened, a glass tube was lowered over a vertical finger

of the sponge so that the tube protected the length of the finger from the laterally impinging current but was at no place in contact with the finger (Fig. 9). The water in this tube on examination was found to be for the most part quiet; its condition, however, did not interfere with the slight currents produced by the sponge itself. Although the osculum of the finger under examination was fully open when the tube was lowered over the finger, it closed in seven minutes after the tube was in position and remained so for a quarter of an hour. A small tube was now inserted into the upper end of the large tube surrounding the finger and a gentle current of seawater was run down into the water surrounding the finger. In fourteen minutes the osculum was again fully open. On cutting off the current the osculum closed in six minutes. It is noteworthy that during the time of these experiments the oscula in the immediate neighborhood of the one tested showed no changes in reference to those observed in the individual within the tube, but they remained for the most part continuously open in the general current of seawater.

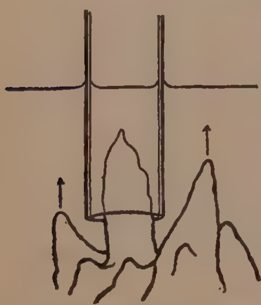


Fig. 9.—Fingers of *Stylotella* in a strong current of seawater. One finger is protected from the current by having a glass tube lowered over it and its osculum in consequence is closed; the oscula of the other fingers are open and emit currents as shown by the arrows.

The next question that naturally suggested itself was how much of a finger must be exposed to a current of seawater to induce the opening of its osculum. To test this, a glass tube was made to cover the distal half of a finger, leaving the proximal half exposed to the general current. To check the eddying of the current up into the tube a

small ring of cotton-wool was inserted between the free end of the tube and the sponge. Under these conditions the osculum closed in eight minutes even though the lower half of the finger carrying the osculum was in a strong current of seawater. This form of experiment was repeated with only the distal fourth of the finger protected from the current, and again the osculum closed in seven minutes. Thus it is only necessary to have quiet water around the outermost fourth of a finger to cause its osculum to close, and a strong current on the proximal three-fourths of the finger will not induce the osculum to open.

FIG. 10.—A finger of *Stylotella* protected from a gentle current of seawater by having a piece of brass-tubing lowered over it and the interspace between it and the tubing filled with cotton-wool. The current impinges only on the tip of the finger, whose osculum nevertheless has opened and emits a current of water, as indicated by the arrow.

These experiments were next reversed and attempts were made to ascertain how much of the distal tip of a finger must be exposed to a current to induce the opening of its osculum. In making these trials, a piece of light-weight brass-tubing was cut to such a length that when it was slipped down over a vertical finger of the sponge, it covered the finger all but the tip (Fig. 10). The space between the oscular tip and the tube was filled with cotton-wool and the whole allowed to stand in quiet seawater. After the osculum had been closed for about a quarter of an hour, a gentle current was started across the end of the tube so that it impinged on only the oscular membrane. In three minutes the osculum showed signs of opening and in eight minutes it was fully open. This form of experiment was many times repeated with essentially similar results. The closing of

the osculum in quiet water and its opening in a current of water are both very local reactions and cannot be induced from points half a centimeter distant on the finger.

If the oscula of *Stylotella* close simply because the water in contact with them ceases to move and not in consequence of the accumulation of waste or lack of oxygen, they probably close in the air on a falling tide because of the same mechanical conditions. If, in the laboratory, an inverted test-tube full of air is lowered over a finger whose osculum is open till the oscular membrane just comes in contact with the air, the osculum closes in about three minutes. The same result can be obtained when the test-tube contains washed hydrogen in place of air. Hence this reaction is not due to the oxygen of the air, but is very probably induced by a purely mechanical condition of quiescence into which the tip of the finger passes in going from the water into the gas.

If a finger of *Stylotella* is cut off about a centimeter from the osculum, that aperture even in a current of seawater is likely to close within a short time and to remain closed for an hour or more. If the finger is cut off at two centimeters from the osculum, there is less likelihood of the closure of the osculum than when the finger is cut at one centimeter. If a pin is stuck into a finger at one and a half centimeters from the osculum, this opening will close in about ten minutes. Thus injury to an adjacent part will bring about a closure of the osculum. The nature of the stimulus produced by injuring the flesh of a sponge seems to be rather mechanical than otherwise. Such an injury besides disrupting the tissues mechanically does little more than liberate their juices. These juices, however, when collected and discharged on a normal sponge with open oscula do not cause the oscula to close. Hence

the closure of the oscula on injury to the sponge is probably due to a mechanical rather than to a chemical stimulation.

Oscula close in running seawater containing small amounts of ether (1/200), chloroform (1/200), strychnine (1/15,000), cocaine (1/1000), and in deoxygenated seawater. They contract, but do not close, in dilute seawater and at temperatures higher than normal, 35 to 45 degrees centigrade. They remain open in currents of seawater after which their closure is inhibited by cocaine (1/10,000) and by atropine (1/1000), as well as by fresh water. Their activities are apparently not controllable by low temperatures, 25 to 9 degrees centigrade, by light, nor by weak solutions of cocaine (1/50,000) and of atropine (1/10,000).

On the inner face of the oscular collar of *Stylotella,* there is a conspicuous sphincter whose contractile cells or myocytes are in many cases so close to the cavity of the osculum as to be in direct contact with the water passing through it. It is probable that the epithelial lining of this region of the osculum is made up of elongated encircling and contractile epithelial cells such as Wilson has shown to occur in the main efferent canals of this sponge. This sphincter is doubtless responsible for the closure of the osculum which may open in consequence of the contractility or of the elasticity of the surrounding flesh. The fact that the osculum closes in from about three to eight minutes after the application of the stimulus and that it opens in from about seven to fourteen minutes when placed in running water shows that the sphincter is a more rapid and efficient mechanism than that concerned with the process of opening which after all may depend upon simple elasticity. Thus the closing and opening of

the osculum is accomplished by one set of contractile cells, in the nature of primitive muscle, working against another set of contractile cells or even against simple tissue elasticity. In this respect the motor mechanism of the osculum is more uniform than that of the dermal pores, for in the osculum there is no pore membrane. In the osculum as in the dermal pore, the active mechanism is apparently directly stimulated and exhibits, therefore, another instance of independent effectors normally called into action by direct stimulation.

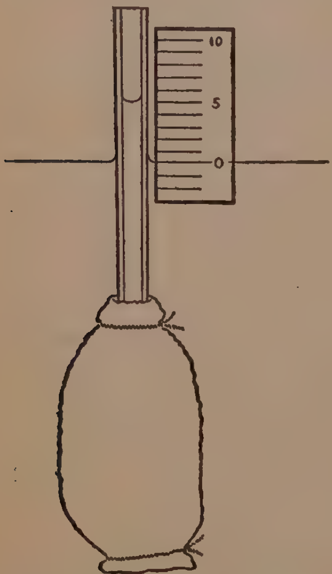


FIG. 11.—Diagram of the apparatus for measuring the strength of a current of seawater produced by *Stylotella*. A finger of this sponge, whose currents were in full activity, was tied off at the base and firmly attached at the tip to a vertical glass tube into which it discharged seawater. The seawater in the tube rose to a higher level than that of the outside water in consequence of the strength of current produced by the sponge. This strength of current could be measured by an attached scale.

The water currents produced by sponges are dependent upon the activity of their flagellate cells or choanocytes, and these cells apparently beat on unremittingly and incessantly. There is no reason to suppose that they ever stand still or reverse their direction of stroke. The only control over these currents seems to be the opening and closing mechanisms of the dermal pores, oscula, and other like devices. It has, however, been suggested that the currents are too considerable to be checked thus and that other means of control must be present. The strength of the water current from *Stylo-*

tella can be easily tested by tying into its osculum a glass tube of appropriate caliber and by allowing the sponge to work till the column of water in the tube comes to a constant level (Fig. 11). By attaching a millimeter scale to the tube this level can then be read, after which the sponge, without disturbance to the apparatus, can be cut off from the tube and the level to which the water in it drops can again be read. The difference between these two readings gives the water pressure generated by the sponge. In *Stylotella* this proved to be between 3.5 and 4.0 millimeters. The current produced by *Stylotella,* then, has a maximum pressure equivalent to a column of water 3.5 to 4.0 millimeters in height (Parker, 1910 *a*).

Determinations of the current strength on seven species of Bermuda sponges gave somewhat lower results as shown in Table 2. In these sponges the average pressures

TABLE 2

CURRENT PRESSURE IN MILLIMETERS OF SEAWATER AS EXHIBITED BY SEVEN SPECIES OF SPONGES FROM THE BERMUDA ISLANDS

Name of Sponge	Height of Column of Seawater in Millimeters for five determinations					Average Height
Tethya	2.5	2.0	2.5	2.0	2.0	2.2
Spirastrella	2.5	2.0	2.0	2.5	2.0	2.2
Pachychalina	1.0	2.0	1.5	1.0	1.0	1.3
Spinosella	3.0	2.5	3.0	3.0	3.0	2.9
Tedania	2.0	2.0	2.5	2.0	2.0	2.1
Stelospongia	2.5	2.0	2.0	2.0	2.0	2.1
Hircinia	3.0	3.0	2.0	2.5	3.0	2.7

of the currents varied from 1.3 to 2.9 millimeters of water. It is therefore clear that the pressure of the currents produced in sponges is very inconsiderable.

The volume of these currents, however, is relatively great and has been determined roughly for *Spinosella* by the following method. A glass tube of known caliber

was tied into the osculum of this sponge, and the sponge and tube submerged in an aquarium. The flow of water through the tube was then determined by measuring the velocity of floating particles, such as grains of carmine, that were carried up the tube by the water current. This proved to be very nearly 4 millimeters a second. As the diameter of the glass tube was 17 millimeters, the osculum must have discharged a little over 0.9 of a cubic centimeter of water a second. At this rate the discharge would amount to some 78 liters a day. As an ordinary *Spinosella* may have as many as twenty such oscula, a colony such as this would have to pass through its substance in a day about 1575 liters of seawater, or over 45 gallons. Sponge currents, therefore, are considerable in volume but low in pressure (Parker, 1914 *c*).

This lowness in pressure, which is rather in contrast with the former belief as to the character of these currents, is favorable for their easy control by the closing and opening devices at the dermal pores and oscula. The adequacy of these devices has been tested in only one instance, the dermal pores of *Stylotella*. A finger of this sponge, in which the dermal pores were closed, was tied to the small end of a glass tube which was bent in the form of a siphon and was so placed that the end carrying the sponge was in one vessel of water and the other end, quite free, was in another vessel of water (Fig. 12). The water in these two vessels was kept at the same level. After the whole apparatus was set up, the water in which the sponge rested was deeply colored with methyl green. The vessel with uncolored water was then lowered till the difference in level between the water contained in it and in the other vessel was sufficient to break through the pores, a state of affairs that could be recognized by the passage

of the deep greenish water up one arm of the siphon. The difference in level was then measured and in eight trials it was found to be between 10 and 15 millimeters. Thus the actual resistance of the closed pores is much more than is necessary to hold in check a current whose maxi-

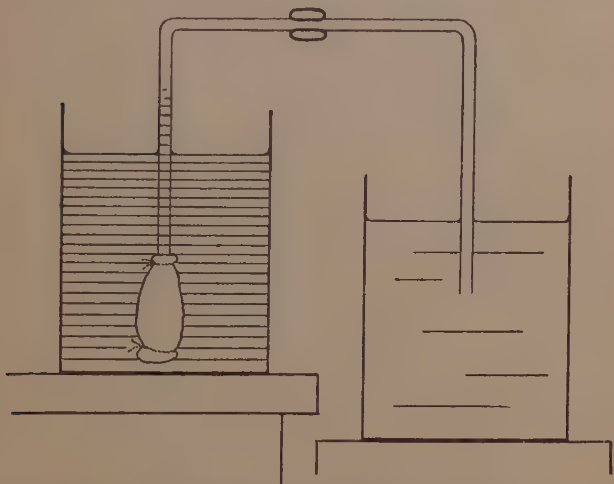


FIG. 12.—Diagram of the apparatus to test the strength of the dermal pores of *Stylotella*. A finger of *Stylotella* with closed pores was attached to a glass siphon tube connecting two vessels of seawater which in the beginning were at the same level. After the apparatus was in position some methyl green was dissolved in the water of the vessel in which the finger was. The other vessel was then lowered till the difference in pressure between the water in the two vessels caused that in the first vessel to break through the pores of the sponge and pass over into the other vessel as was indicated by the appearance of the colored water in the siphon tube. The difference in the levels of the water in the two vessels was then measured and thus the pressure necessary to open the dermal pores of the sponge was determined.

mum suction is represented by a pressure of not over 4 millimeters of water (Parker, 1910 *a*).

Notwithstanding the fact that the opening and closing mechanisms of the dermal pores and oscula in sponges involve independent effectors in the form of primitive muscle cells, it would be quite erroneous to ascribe to these animals a complete absence of transmission. It has already been pointed out that if an injury, for in-

stance by cutting, is inflicted on a finger of *Stylotella,* it will, if not too far away, call forth a temporary contraction of the osculum. This does not occur commonly when the injury is two centimeters from the osculum, but it does occur with great regularity when the injury is within one centimeter of that aperture. What it is that is transmitted from the seat of injury to the contractile tissue about the osculum is by no means clear. That it is not due to escaping juices from the wound has already been shown. It may be brought about by a slow progressive contraction of the flesh which, starting at the wound, gradually creeps to the sphincter, or it may be a slow progressive transmission unaccompanied with any real contraction. Such a transmission as that first mentioned would be in the nature of a progressive muscular wave whereas that last suggested would partake of the essentials of a sluggish nervous transmission. Which of these two methods occurs in *Stylotella* cannot at present be stated, but that there is in many tissues a sluggish transmission unaccompanied with observable motion and, therefore, nervelike is beyond question. Such neuroid transmission, limited in the extent over which it may spread, is in all probability to be attributed to sponges. It is in all likelihood the form of transmission characteristic of the continuous protoplasm of such forms as the protozoans. This transmitting capacity is so undifferentiated and so limited in its power to spread that while it may be looked upon as the germ from which nervous transmission has grown, it cannot be said to be a sign of nervous tissue. In consequence of the absence of effective transmission in sponges the various effector elements of these organisms lack coördination almost completely. Thus, as already stated, the closure of one osculum through the local ap-

plication of appropriate stimuli to it, has no effect on the neighboring oscula. It must, therefore, be admitted that the physiological findings agree with the histological results in supporting the conclusion that sponges are devoid of true nervous elements (Minchin, 1900).

Sponges, then, represent that stage of evolution in which a primitive type of muscle tissue has made its appearance unaccompanied with nervous elements. To state this conclusion in the terms used in the earlier part of this discussion, sponges may be said to have among their cell combinations effectors, but no receptors or adjustors. They mark the beginnings of the neuromuscular mechanism in that they possess the original and most ancient of its constituents, muscle, around which the remainder of the system is supposed subsequently to have been evolved (Parker, 1909, 1910 *b*, 1911, 1914 *b*).

CHAPTER IV

INDEPENDENT EFFECTORS IN HIGHER ANIMALS

If sponges possess effectors, such as muscular sphincters, that are not innervated, but that become active in consequence of direct stimulation, and if these animals exhibit at best a low degree of transmission such as that designated as neuroid, it is not improbable that these conditions may persist locally or be revived in the organization of the more differentiated animals. At least a search for such instances may not be an unprofitable one.

From the standpoint of musculature it may be asked whether the more differentiated animals possess muscles that are directly stimulated normally or, to go one step further, that act with complete independence of nervous control? Such muscles would simulate in many respects those believed to exist in sponges. Evidence in favor of this possibility has been brought forward within recent years in connection with the sphincter of the vertebrate iris. The contraction of the pupil of the eye in bright light is a well-attested fact and has long been recognized as an example of simple reflex action in which the afferent course is through the optic nerve and the efferent one through the oculomotor nerve. Nevertheless, the sphincter of the pupil also seems to act under direct stimulation.

Arnold, as early as 1841, observed that in the eye of the eel the pupil contracted in bright light even after that organ had been removed from the fish's head. And Brown-Séquard subsequently confirmed this observation and showed that when the eye was cut in half vertically,

the hemisphere containing the iris still continued to exhibit this contraction. He concluded, though on insufficient grounds, that the sphincter of the pupil was acted on directly by the light. The belief that this reaction was due to an intraocular reflex and not to the direct action of the light on the muscle concerned was shown to be extremely improbable by Steinach (1892), who worked on a number of lower vertebrates, but especially on the frog and eel. Steinach found that when the half of the bulb containing the iris was cut down to the extreme by removing the edges of the retina and the ciliary body, the reaction still took place. Moreover, if a very small intense point of light was focussed on the iris, the portion of this organ thus illuminated was the first part to begin to contract and this activity spread from the region thus stimulated to the adjacent regions. A histological investigation of the contracted iris showed that the elements concerned in this contraction were the pigmented smooth muscle cells of the sphincter pupillæ, whose pigment absorbed precisely those rays, the shorter wave lengths, that had been found to be especially stimulating. Steinach, therefore, concluded that in fishes and amphibians the smooth muscle elements of the sphincter pupillæ may be directly stimulated by light.

The objection to this conclusion raised by Magnus (1899) to the effect that the reaction could be prevented by atropin, though the sphincter would still respond to electrical stimulation, was shown by Guth (1901) not to be well founded. Guth, moreover, was able to demonstrate a contraction in the sphincter nearly two weeks after the eye had been cut out, a period much too long for the persistence of an intraocular reflex mechanism in an organ thus removed from the body. He also was able to

produce contraction by the strong illumination of small groups of muscle fibers isolated from the sphincter. The application of Steinach's conclusions to the iris of the cephalopod eye, to that of birds, in which the sphincter is composed of cross-striped muscle fibers, and even to mammals was made by Nepveu (1907).

Steinach's investigations, however, received their fullest confirmation from the work of Hertel (1906), who studied not only the eyes of the lower vertebrates but those of the higher forms including even man. As a means of stimulation Hertel used light from an electric arc, from a gas flame, and diffuse daylight. After the optic nerve had been cut, the iris in the eye of the eel and of the frog contracted to all three lights, whereas that in the eye of the cat and the rabbit contracted only to the arc light, a condition also observed in human beings who had suffered a degeneration of the optic nerve. In the three mammals thus tested a pencil of strong light could be thrown through the pupil into the fundus of the eye without producing any contraction, though as soon as this pencil was brought to bear on the edge of the iris a local contraction was observed. Hertel, therefore, concluded that the contraction of the pupil in blinded eyes was not due to an intraocular reflex but to direct stimulation and that this occurred in the eyes of mammals as well as in those of the lower vertebrates. The mammal iris, however, appeared to be less easily stimulated in this way than that of the fish or the amphibian, for it did not react to the weaker lights, gas light and daylight, to which the others were freely responsive. Thus Hertel's observations completely confirmed as well as extended those of Steinach.

The sphincter pupillæ of the vertebrate eye, and prob-

ably also that of the cephalopod eye, may, therefore, be regarded as muscles normally subject to direct stimulation by light, notwithstanding the fact that they are also under nervous control. In so far as this type of muscle is open to direct stimulation, it reproduces the condition found in sponges where a superficial sphincter is also the form assumed by the muscle in question. Whether in addition to stimulation by light the sphincter pupillæ in vertebrates is open to direct chemical stimulation, as might be inferred from the work of Auer and Meltzer (1909) on calcium, remains still to be definitely decided.

Although the sphincter in the iris of the eye appears, therefore, to be a muscle normally subject to direct stimulation, and in this sense illustrates the principle of an independent effector, the muscle that has been most discussed from this standpoint is that of the vertebrate heart. In general two opinions have been held respecting the cause of contraction in this muscle. According to one view, the myogenic theory, the beat of the heart is brought about through changes that are initiated in the heart muscle itself. According to the other view, the neurogenic theory, the impulses to rhythmic beating originate in nervous tissue and are delivered secondarily to the heart. The myogenic theory implies that this muscle is essentially an independent effector not unlike the muscular organs of sponges. The neurogenic theory places the heart muscle under nervous control, as most of the muscles in the higher animals are.

These two theories of the nature of the heart-beat have had a long and complicated history, which has been well reviewed by Engelmann (1904) and by Howell (1906). It will, therefore, not be necessary in the present connection to enter into this side of the subject beyond stating

that of recent years the myogenic theory, which took its origin in the very early work of Harvey, has on the whole gained precedence (Lewis, 1917) and that this is chiefly due to the work of Gaskell, Engelmann, and their followers. According to these investigators the heart in the lower vertebrates is a muscular tube bent in the form of a letter S and dilated into a series of four chambers (Fig. 13). The heart becomes complicated in the higher forms

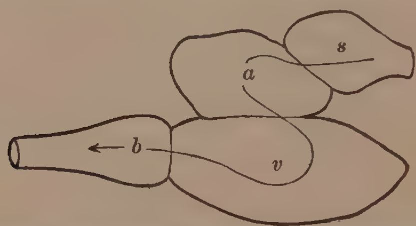


FIG. 13.—Diagram of the heart of a fish showing in lateral view its four chambers, the venous sinus *s*, the auricle *a*, the ventricle *v* and the bulb *b*. The s-shaped axis is indicated by the arrow.

chiefly through the appearance of a set of partitions whereby this organ is divided into right and left halves. Contraction normally begins in the muscle of the most posterior chamber, the venous sinus, or when this chamber is incorporated in the next chamber in advance, the auricle, in the muscle of the posterior portion of this chamber of the heart. The spot in which contraction originates is called in the hearts of the higher vertebrates the sino-auricular node. From this node the wave of contraction spreads over the auricle and across the narrow bridge of muscle, to the ventricle. Here it is rapidly propagated by the specialized muscular tissue of the inner face of the ventricle, the so-called Purkinye tissue, over the whole of this part of the cardiac muscle, which is thus brought into a unified contraction. According to this view contraction arises in the muscle itself and is

propagated as a wave from the venous to the arterial end of this organ.

The discovery by Remak in 1844 that the heart muscle of vertebrates contains an abundance of nerve cells has been used as a strong argument in favor of the neurogenic theory. But it is now generally believed that these cells are merely concerned with modifying a heart-beat which in its origin is myogenic. From this standpoint, therefore, the presence of these nerve cells affords no serious obstacle to the acceptance of the myogenic interpretation of the heart-beat, but it does leave the adult vertebrate heart a less clear example of an independent effector than might be desired.

Although in this respect the adult heart falls short of all that might be wished, the embryonic heart of vertebrates is quite otherwise. In the developing chick the heart is the first complicated organ to assume functional activity. It arises after about twenty-three hours of incubation and it begins to pulsate about six hours later. At this step in the development of the chick, the stage of ten somites, the neural crests are not yet formed and neuroblasts are not yet differentiated. Hence there is every reason to believe that the heart is absolutely free from possible nervous influence and that its beat must be purely myogenic. Not until some time after the heart has been in action, in the chick on the sixth day of incubation, is this organ first invaded by nerve cells, a condition also to be observed in a number of other vertebrates (His, 1893). Hooker (1911) has likewise shown that in frog embryos from which the developing nervous system has been removed, the heart not only differentiates but eventually beats, a condition that confirms the older results on the chick. Hence the early embryonic heart in

vertebrates must be admitted to have a purely myogenic beat and at this stage to be an absolutely clear instance of an independent effector such as is shown in the muscles of sponges.

If further grounds were needed to support the opinion that the embryonic vertebrate heart has a myogenic beat, they can be found in the work of Burrows (1912), who cultivated the heart muscle from chick embryos *in vitro.* Pieces of the beating heart of young embryos were transferred to culture fluids where they became centers of outgrowths of cells. In time many of these cells began rhythmic beating at a rate of 50 to 120 beats per minute, a rhythm typical for beating pieces of the ventricular muscle. As some of the beating cells were absolutely disconnected from the rest of the tissue, they afforded most conclusive evidence of myogenic activity. These unicellular mechanisms are models, so to speak, of the embryonic vertebrate heart, whose nature as an independent effector is thereby exemplified. The independent rhythmic contraction of skeletal muscle has also been demonstrated through this method by Lewis (1915).

The modes of action of the heart muscles of other animals than the vertebrates present considerable diversity. Thus Carlson (1904) has shown that in the King crab, *Limulus,* the heart-beat is purely neurogenic and is as dependent on extraneous nerve centers as are most other arthropod muscles. On the other hand, the heart of the silkworm is said by Pigorini (1917) to continue to beat even after it has been separated from the central nervous system and cut into isolated segments, a condition that is also claimed for the heart in tunicates.

The tunicate heart, in consequence of the remarkable periodic reversal in the direction of its beat, has excited

the attention of investigators for many years. The organ itself is in the form of a swollen tube, one end of which is continuous with the blood-vessels distributed to the viscera and the other with those distributed to the gills (Fig. 14). The action of the heart, the reversal of which

A

B

FIG. 14.—*A*. Diagrammatic view of a longitudinal section of *Salpa* (after Herdman) showing by arrows the inlet or branchial aperture and the outlet or atrial aperture as well as the position of the heart *h*. *B*. Enlarged view of an isolated heart of *Salpa* showing the abvisceral end *g* connecting with the gills and advisceral end *v* running to the viscera.

was apparently first observed by Van Hasselt in 1821, consists in a series of advisceral beats, by which the blood is driven toward the viscera, followed by a series of abvisceral beats, by which it is driven toward the gills. The relations of these sequences of beats have been extensively studied by Schultze (1901) in *Salpa*, and more recently by Hecht (1918) in *Ascidia*.

It is commonly believed that in these pulsation series the advisceral equal the abvisceral beats, but a closer examination of the facts shows that in general the ad-

visceral beats predominate. There seems to be no question but that in the heart of the tunicate there are two centers from which contractions may arise, one at the advisceral and the other at the abvisceral end. It is apparently the alternate control of the heart by first one and then the other of these centers that brings about the reversal in the activity of this organ (Loeb, 1899, 1902).

Whether these two centers are located in the muscle of the tunicate heart or in other tissue connected with this muscle is somewhat uncertain. The heart itself is commonly described as made up of a single layer of muscle cells whose inner face is covered with a delicate endothelium. Nerve cells have been supposed by most investigators to be entirely absent, but Hunter (1902) claimed to have identified them in *Molgula,* where they are said to be especially abundant at the two poles of the heart, the regions from which the contraction waves start. Their presence is also mentioned by Alexandrowicz (1913). The observations that the isolated middle portion of the heart, where nerve cells are very sparse, if in fact they are present at all, will continue in rhythmic contraction (Schultze, 1901; Bancroft and Esterly, 1903; Hecht, 1918) even after it has been isolated and placed in seawater suggest that these cells have no more to do with originating this form of heart-beat than the similar cells in the vertebrate heart have. Hecht (1918) has also pointed out that in perfectly normal specimens of *Ascidia* the contraction wave in the heart muscle may sometimes originate in this middle portion of the heart, showing that this part may normally act as a pacemaker for the whole organ and that its action in isolation is, therefore, nothing unusual. It has also been determined that the rate of transmission of the contraction wave over the

heart of *Ascidia* is relatively slow, 1.76 to 2.12 centimeters per second, a rate more in accord with muscle transmission than with nerve transmission (Hecht, 1918). The heart of the tunicate, therefore, appears to be like that of the adult vertebrate, an independent effector complicated in a secondary way by the presence of nerve cells.

According to the investigations of Lewis and Lewis (1917) the amnion of the embryo chick is an organ that exhibits all the characteristics of an independent effector. This membrane is composed of a single layer of mesenchyme cells overlaid by a single layer of epithelial cells. The mesenchyme cells differentiate into smooth muscle cells that undergo definite contraction as early as the fourth or fifth day of incubation. So far as is known, there is no nerve supply to the amnion. Hence contractions in the smooth muscle layer in this organ must be excited by the direct stimulation of its fibers. This view is supported by the fact that in tissue cultures made from the amnion there can be easily found in the outgrowing cells after a day or two groups of smooth muscle fibers or even single fibers that exhibit rhythmic contractions. These are absolutely devoid of nervous connections and must, therefore, be stimulated directly, a conclusion that is supported by the fact that after they have ceased to contract rhythmically they can be re-excited to this activity by washing them with a drop of fresh culture medium to which an excess of calcium has been added. There is, therefore, every reason to believe that the smooth muscle layer of the amnion of the chick is an independent effector.

The instances of this peculiar type of tissue thus far noticed in animals above the sponges have been taken from the higher animals and almost entirely from the vertebrates. This is due to the fact that since these

animals have been much more fully studied than the lower ones, examples of this rather novel condition are better known among these more differentiated types than among the simpler forms. It is probable that a close examination of the lower invertebrates will disclose many such instances. Thus in the sea-anemone *Metridium* the circular muscle of the column is very much like that in the vertebrate iris in that it is both under nervous control and open to direct stimulation. This sea-anemone, like most other members of its group, is a somewhat cylindrical animal, one end of which is attached to some firm object in the sea and the other provided with a ring of tentacles that surrounds a centrally located mouth. The circular muscle of the column is a sheet of muscle whose fibers invest in a circular fashion the inner face of the cylindrical outer wall of this animal (Parker and Titus, 1916). If this muscle contracts locally it produces a ring-like constriction around the animal's body. In sea-anemones that have been well fed recently, constrictions of this kind form near the oral end of the animal and pass down the cylindrical column of its body to the opposite end. They may recur every four or five minutes and resemble in a general way the peristaltic waves of the intestine. They are probably concerned with the movement within of the newly acquired food, for they occur almost invariably after extensive feeding. It is probable, though this is not definitely proved, that the peristalsis just described is coördinated by the nerve-net contained within the wall of the sea-anemone's body.

If an area on the outer surface of this wall is thoroughly anesthetized by allowing crystals of magnesium sulphate to dissolve on it, it can be easily rendered so insensitive to touch that the typical contraction of the ani-

mal as a whole can no longer be called forth by prodding it. Nevertheless, such stimulation will induce a sharply defined ring of constriction to arise from the spot stimulated and pass slowly round the column. As this experiment succeeds even after the sea-anemone is deeply and fully anesthetized, the contraction of the muscle must be ascribed to direct stimulation. Hence the circular muscle of the column in *Metridium*, though partly under nervous control, is certainly open to direct stimulation, and from this standpoint represents an independent effector (Parker, 1916 *a*).

A fuller instance of this condition is seen in the acontial muscles of the same sea-anemone, *Metridium*. This sea-anemone, in common with many other closely related forms, carries within its body great numbers of delicate thread-like filaments, the acontia. These acontia, which may be as much as four or five centimeters long, are attached by one end to the mesenteries in the interior of the sea-anemone's body. Ordinarily the acontia are more or less coiled up within the digestive cavity of the animal. When for any reason the sea-anemone is made to contract vigorously and the water contained within its central cavity is thus driven out, the acontia stream with the current of water in great profusion out of the mouth and out of the lateral pores, or cinclides, by which the digestive cavity is put into direct communication with the surrounding seawater. Thus the contracting sea-anemone throws out over its body a protecting system of filaments, for these living threads are armed with the most vigorous nettling cells of any in this animal and will effectively sting an unwary intruder. As the sea-anemone gradually expands again by taking water into its body, the acontia are slowly drawn back and eventually returned

to their original position in the interior of the animal. This withdrawal is accomplished chiefly by the action of the cilia on the acontia, which form an extensive band on each of these filaments and beat in such a direction as to carry the acontium through the seawater toward its attached base.

When the acontia are fully extended in the external seawater, and perhaps also after they are withdrawn within the sea-anemone, they may exhibit more or less continuous, slow, serpentine movements. These movements are due partly to their cilia and partly to a strand of muscle fibers that extends lengthwise their axial region and is known as the longitudinal muscle of the acontium. It has been claimed that this acontial muscle has parallel and close to it a delicate band of nervous tissue, but, for the following reasons, this does not seem to be true. Pieces of acontia four to five centimeters long can be easily obtained from a large sea-anemone and will continue alive and active in seawater for many hours. When such filaments are mechanically stimulated by agitating them in seawater or by dropping seawater on them, or when they are flooded with dilute meat juice, they twist themselves into irregular coils. This response takes place slowly and only after a minute or two. If the stimulus is limited to one end of a long acontium that end and that end only responds by becoming coiled. This reaction will occur as well at the central end as at the peripheral end of a given acontium. When acontia have been kept for twenty minutes or so in seawater containing chloretone, a period long enough to anesthetize the tentacles of an intact sea-anemone, they will still become coiled when flooded with dilute meat juice exactly as unanesthetized acontia do. When acontia still attached to a sea-anemone,

but extending several centimeters away from it, are variously stimulated at their free ends, not the least response has ever been observed in the sea-anemone itself, though the acontia react vigorously in the region to which the stimulus is applied. The stimulation of their free ends seems to have no more influence on the sea-anemone than the cutting of the free end of a long hair has on a human being. From these observations it seems fair to conclude that the acontia of sea-anemones are devoid of nervous structures and that their longitudinal muscle must, therefore, be stimulated directly as an independent factor (Parker and Titus, 1916).

From the instances thus far given it is evident that independent effectors in the form of muscles occur among the most differentiated as well as among the simplest of the multicellular animals. The capacity of these effectors to be stimulated directly is only another aspect of what physiologists have long recognized in respect to ordinary muscle, namely, the great ease with which such tissue can be directly stimulated by almost any agent. The number of these independent effectors will doubtless increase as the animal series is more fully investigated. Some of those already noted, like the acontial muscles of sea-anemones, may be survivals of that primitive state seen in the sponges; others, like the muscle of the embryonic heart in vertebrates, may be special adaptations newly brought into being by the exigencies of the particular situation. But however this may be, these examples all point to the principle that of the three elemental constituents of the neuromuscular mechanism, the sense organ, the central nervous organ, and the muscle, the only one that can be thought of as existing independently is the muscle, and that this, therefore, is the most primitive of the three.

CHAPTER V

NEUROID TRANSMISSION IN HIGHER ANIMALS

Although sponges give no evidence of possessing any true nervous tissue and have at most only independent effectors in the form of muscles, it would be a mistake to assume that they are devoid of everything that is in any sense nervous in nature. It has already been pointed out that if a finger of the sponge *Stylotella* is cut into within a centimeter and a half of the osculum, this aperture will usually close after some minutes. The sluggish transmission upon which this reaction depends represents without doubt that elemental property of protoplasmic transmission from which true nervous activity has been evolved. It may, therefore, not inappropriately be called neuroid transmission. This elemental type of transmission probably occurs in many tissues of the higher animals, but it is by no means easily detected, for most tissues are incapable of those activities by which such transmission could be indicated. Favorable conditions for its study, however, are found in one type of epithelial tissue, namely, ciliated epithelium. This tissue is not only freely open to stimulation, but it possesses in its cilia convenient parts of an effector kind by which its responses to stimulation can be shown. Extended ciliated fields are, therefore, favorable grounds for the study of neuroid transmission.

The structure and function of ciliated cells and epithelia have been reviewed recently by Pütter (1903), by du Bois-Reymond (1914), and especially by Prenant (1912-1914), and an extensive and original investigation

of these elements has been carried out by Saguchi (1917). Some of the earlier workers advanced the opinion that at least among certain invertebrates cilia were under the control of the nervous system, and Apáthy (1897) went so far as to claim that the intracellular fibrillar system of the ciliated cell was nervous, though he never succeeded in demonstrating a connection between this system and nerves. The fact, however, that no one has ever been able to control ciliary activity through nerves and that all the cases of ciliary coördination thus far brought forward can be explained on the basis of neuroid transmission renders the belief in the nervous control of cilia extremely improbable. In fact, it may be stated that at present there is not the least ground for the assumption that true nervous activity is in any direct way involved in ordinary ciliary reactions. Yet notwithstanding this independence of ciliated and nervous tissues, the coördination in the activities of a ciliated field is one of its most striking features.

If the ciliated epithelium from the palate of the frog is placed under a microscope, the various foreign particles lying on its surface will be seen to be swept along in a definite and constant direction, in this particular instance toward the œsophageal end of the tissue. The ciliated field, moreover, will reproduce in its appearance almost exactly the aspect of a field of grain over which a gentle wind is blowing. The direction of the undulations in this field agrees with that in which the particles are borne along.

When these appearances are further examined, they are found to depend upon two factors, the direction of the effective stroke of the cilia and the sequence of these strokes. The direction in which the particles move is

due to the direction of the effective stroke of the cilia. Each cilium moves back and forth on a fixed base. In its forward or effective stroke the cilium acts in such a way as to drive the supernatant fluid and its suspended particles along with it. In its backward stroke or recovery the cilium returns to its former position, imparting as little motion to the surrounding fluid as possible. Thus each effective stroke moves the superimposed fluid forward and each recovery leaves this fluid in large part standing. Hence in general the fluid moves on in one direction only, namely, that of the effective stroke.

The second factor in the ciliary activity of the frog's palate is shown in the sequence in which the successive cilia beat. In this particular example, as in most other ciliated membranes, the cilia do not beat all at the same moment or synchronously, but in regular order one after another, or metachronously. Thus after one cilium has begun its effective stroke the next cilium in the direction of this stroke takes up the activity, and so on till the wave has passed over the whole field. Thus the cilia of a given membrane do not act independently nor in unison but in sequence, and thus exhibit a high degree of coördination. It is this metachronous coördination that gives to the ciliated membrane the appearance of a field of grain over which a wind is blowing.

The two elements of ciliary action that have thus been pointed out, though of necessity intimately associated, are in truth quite independent of each other. Their independence is perhaps best indicated by the fact that there are instances in which their directions are opposed instead of being in agreement, as in the epithelium of the frog's palate. One of the best of these is seen in the swimming plates of the ctenophores (Fig. 15). In these

animals the swimming plates form eight well-defined rows that extend from the aboral pole toward, if not actually to, the oral pole. The effective stroke of each plate is in the aboral direction, thus carrying the animal through the water with its mouth forward. The wave of ciliary action, however, sweeps over each row from its aboral to its oral end and thus takes a course the reverse of that indicated by the effective stroke. Hence it may be concluded that the effective stroke and the wave of ciliary action are independent factors; for though they usually agree in direction they may be directly opposed as in the example just given.

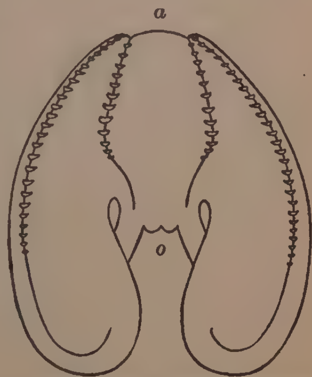


FIG. 15.—Side view of the ctenophore *Mnemiopsis leidyi*. Of the eight rows of swimming plates four are shown, two long ones and two short. All start from the aboral pole *a* and converge on the oral pole *o*.

The regularity with which one cilium beats after another, the coördinated metachronism of the series, is the feature of the ciliated epithelia that most recalls nervous control and that requires explanation. It might be supposed that this regularity was due to the mechanical influence of a given cilium on the one next following and so forth. Thus if cilium A begins to beat, it will strike toward cilium B, which on being struck will thus be called into action and by a similar process excite C and so on. This operation, at least so far as the effective stroke is concerned, is not unlike that seen in the successive toppling over of a row of bricks each on end where the fall of the first brick knocks over the second and so on. Although this explanation finds an easy application to the usual form of ciliary beat in which the effective

stroke is in the *same* direction as the general wave, it is not so easily applied to cases where, as in the ctenophores, the reverse is true, that is, the effective stroke is in a direction *opposite* to that of the wave of ciliary action. Here the effective stroke of a plate would not be directed toward the one next to act, but toward the one that had just previously acted. Hence the mechanical explanation offered above fails of satisfactory application. For reasons that will be given presently this mechanical explanation can also be shown to be entirely inapplicable also to those cases in which the direction of the effective stroke and that of the ciliary wave agree.

If the wave of ciliary metachronism is not due to the direct mechanical action of one cilium on another, the form of coördination that this process exhibits must depend upon some part of the cell deeper than the ciliated zone. Such might well be the cytoplasm, even the superficial cytoplasm, of the cell itself. Evidence in favor of this opinion was advanced by Kraft as early as 1890.

Kraft showed by two methods of experimentation that stimuli applied to a ciliated field on one side of a band of quiescent cilia could influence ciliary action on the other side of this band, thus demonstrating a transmission over a region devoid for the time being of any form of mechanical activity. The first method of experimentation involved the use of a small temperature box divided into three chambers and so arranged with inlets and outlets that each chamber could be supplied with a current of water of fixed temperature (Fig. 16). These chambers all abutted on one face of the box and thus this face represented a surface on which there might be established three sharply defined areas each with its own temperature. The whole apparatus was of such small size that

a sheet of ciliated epithelium could cover all three areas, and the epithelium was always so placed that the axis corresponding to the direction of its ciliary waves passed over all three chambers. When the two end chambers contained water at 20° C. and the intermediate chamber water at 0° to 2° C., the cilia beat continuously from one end of the membrane to the other. When, however, the temperature of the two end chambers was reduced to from 10° to 12° C., the cilia over these chambers beat at a very slow rate, one to two strokes per second, and those over the middle chamber were entirely quiescent. If now the cilia over the first end chamber were stimulated to greater activity by stroking them gently with a fine brush, increased activity soon appeared in those over the other end chamber, though the cilia over the intermediate region remained entirely motionless. Thus a form of transmission other than that carried out by the mechanical activity of the cilia must be admitted to have taken place over the area between the two extremes.

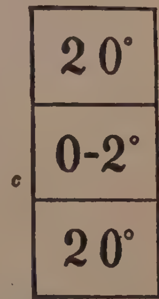


FIG. 16.—Plan of a temperature box divided into three chambers, each of which can be kept constant by a flow of water. The box is of such a size as to allow a piece of ciliated epithelium to be spread over the three temperature areas as in the experiment by Kraft.

A second experimental test was carried out by Kraft with the apparatus just described, but with the use of a temperature not a mechanical stimulus. In this test the two end chambers were set at 10° C. and the intermediate chamber was kept so cold that the cilia over it did not beat. Those over the end chambers beat only slightly. The temperature in the first chamber was then raised from its original point of 10° C. to 15° C. and the cilia over this chamber now began to beat more rapidly than

before. Soon after this increase of activity was noted over the first chamber, a like increase appeared in the cilia over the third chamber, though the cilia in the intermediate region remained motionless. After a time, however, these too began to beat. Kraft concluded, therefore, that a region of quiescent cilia could transmit impulses to increased activity without showing any ciliary movement itself. The subsequent activity of the intermediate cilia he believed to be due to mechanical stimulation received from the especially excited cilia over the first chamber. It is thus clear, as Engelmann long ago maintained, that ciliated epithelia may transmit impulses to action without any associated mechanical disturbance. These impulses pass through the deeper protoplasmic parts of the tissue and call forth the successive activity of the cilia which thus gives evidence of this transmission wave. Such an activity is sufficiently nerve-like in character to justify the designation neuroid.

In ciliated epithelia this type of transmission exhibits a feature long ago recognized by Grützner and especially by Kraft wherein it shows a remarkable resemblance to true nervous transmission in even the more specialized types of central nervous organs. Ciliated transmission is limited as to its spread and direction. If a spot in a relatively quiescent field of ciliated epithelium is mechanically stimulated the increased activity of the cilia thus produced does not spread in all directions over the field, but forms a band beginning at the spot stimulated and extending in the direction taken by the transmission wave. This band may become somewhat wider than the spot as one recedes from the region of stimulation, but it never spreads to any considerable extent. This condition justifies the conclusion that the individual cells in a ciliated

epithelium are somewhat like the neurones in the differentiated central nervous organs in that transmission from element to element is easily accomplished in one direction but not in the reverse. Hence this type of transmission is definitely restricted in its course. That this is a structural feature of ciliated epithelium is shown in the experiment of von Brücke (1916) who demonstrated that when a small piece of ciliated epithelium was cut out and reimplanted after having been turned through a half-circle, it retained after healing the original direction of its effective stroke and its transmission wave was in opposition to that of the surrounding field. Thus whatever it is that determines the polarization of ciliated epithelia, that feature is resident locally in the epithelium itself and is not impressed upon it from some external source.

The facts that have thus far been brought out for ciliated epithelium can also be demonstrated for the most part on the rows of swimming plates on ctenophores. In these animals each swimming plate is like a gigantic flattened cilium. It is compound in nature, for it arises from a group of cells instead of from a single cell; otherwise, it is essentially like a cilium. These plates, as already indicated, form eight well-defined rows, extending over the body of the ctenophore from its aboral toward its oral pole. Transmission waves pass over these rows in an oral direction, but the effective stroke of each plate is in the aboral direction, thus driving the ctenophore through the water mouth foremost. The rows of plates, therefore, like rows of cilia, exhibit a well-developed metachronism. The fact that the plates are often normally quiescent and may become active only at intervals makes them very convenient for experimental work.

If the longitudinal band of tissue to which the plates

are attached in the common American ctenophore *Mnemiopsis* is cut across even in a very superficial way, the ordinary transmission waves can be seen to proceed from the aboral pole over the line of plates orally to the cut, where they cease. Beyond the cut the plates for some time after the operation are in incessant vibration, the waves beginning at the cut end of the series and running to the end near the mouth. The oral course of the transmission wave is so universally characteristic of the ctenophores that the polarity of their rows of swimming plates may be said to be as pronounced as that of the rows of cilia in a ciliated epithelium.

When a spot about midway the length of a row of plates in *Mnemiopsis* is touched, the region about it immediately becomes depressed and the edges of the depression fold over and cover in the plates. This reaction was observed long ago by Verworn (1890) on *Beroe,* and, though it has been questioned by Bauer (1910), the observation seems to be abundantly confirmed by Lillie (1906) and by Kinoshita (1910), who demonstrated further that it could occur on a fragment of a *Beroe* over which the row of swimming plates extended. By this means in *Mnemiopsis,* and probably in a number of other ctenophores, half a dozen plates or so near the middle of a row may become so much restrained that they will not show the least motion. Nevertheless, transmission waves that arrive at the aboral entrance to this depression emerge from its oral end with the greatest regularity. This may happen while the covered region is under the closest inspection through a lens and during which not the least sign of movement can be detected in the restrained plates. Thus the mechanical movement of the swimming plates is no more necessary for the transmis-

sion wave in ctenophores than the movement of the cilia is for a like wave in ciliated epithelia.

When a row of plates in a *Mnemiopsis* pinned out in seawater has passed under it a metal tube of small caliber and is chilled by running water at 4° to 5° C. through the tube, the plates in the region subjected to the cold cease to beat, though transmission waves may be seen to arrive at one edge of the cooled area and to emerge at the opposite edge with regularity. Again the swimming plates resemble cilia in that in an area in which the plates have been rendered quiescent by chilling transmission is still possible.

In handling specimens of *Mnemiopsis* in the experiments last described, it was noticed that when the rows of plates under which the metal tube passed were subjected to a little local stretching by the awkward manipulation of the tube, the plates often ceased to vibrate in the stretched region. On repeating this operation it was found that as a rule the slight stretching of the band of tissue to which the plates were attached would bring the plates of the stretched part to a standstill, though it did not interfere seriously with transmission. In such an operation, however, much care was required not to overstrain the tissue, for otherwise a permanent cessation of action followed. Avoiding this difficulty, however, mechanical strain, like low temperature, may be made to check motion without interfering with transmission. Thus in several ways the swimming plates of the ctenophores exhibit all the peculiarities of rows of cilia (Parker, 1905 *b*).

The bands of tissue to which the swimming plates are attached in ctenophores have been studied with much care, but in no instance have nerve cells been found as-

sociated with them in such a way that their ordinary powers of transmission and polarization could be attributed to these elements. It seems likely that transmission along the bands of plates whereby their metachronism is maintained is accomplished through the epithelial cells that compose the bands as it is in the rows of cells in ciliated epithelia.

Although this view of the coördination of the swimming plates of ctenophores agrees well with the established facts in the case, it must not be forgotten that evidence has been brought forward to show that these plates, unlike ordinary cilia, are under some nervous control and that in this respect they represent a more complex state of affairs than that seen in ordinary ciliated epithelium. This evidence has been produced by Bauer (1910). If a swimming *Beroe* is gently touched in the region of the mouth, its swimming plates momentarily cease moving. If it is vigorously stimulated in the same region by being stuck or cut, for instance, its plates act for a short time more vigorously than usual. Thus a slight stimulus produced inhibition, a considerable one excitation. If now the sense body at the aboral pole of the animal is cut out, thus removing what is usually assumed to be the chief coördinating center for the activity of the rows of plates, the same reactions in the plates recur on applying the appropriate stimuli to the region of the mouth. Bauer, therefore, believes that since these reactions can not be ascribed to the aboral sense body they must depend upon the action of the diffuse nervous system which has long been known as a subepithelial network and which, though chiefly concerned with the muscles of the ctenophore, probably also exerts a secondary influence on its rows of swimming plates. Thus the nervous control of the swim-

ming plates is quite subordinate to that through which their normal activity is called forth and which in all respects agrees with the type of neuroid transmission already described in ordinary ciliated epithelia.

From these examples it appears that the ordinary tissues of animals, at least their ciliated epithelia, may exhibit sluggish forms of transmission that are so like those seen in sponges as to admit of being classed under the single head of neuroid transmission. Such a form of transmission is represented in sponges not only by the closure of their oscular sphincters when a more distant part of the animal is injured, but by their system of flagellated cells whose activity, like that of the cells in a ciliated epithelium, must be coördinated by some such form of transmission. Although of the three identifiable elements of the neuromuscular mechanisms of animals, sense organs, central nervous organs, and muscles, sponges possess only muscles, they nevertheless exhibit among their many activities neuroid transmission, a sluggish form of transmission that may be considered the forerunner of nervous activities, and in this sense may represent the germ from which has sprung the real nervous conduction of the more complex animals.

SECTION II. RECEPTOR-EFFECTOR SYSTEMS

CHAPTER VI

THE NEUROMUSCULAR STRUCTURE OF SEA-ANEMONES

Sponges are animals in whose structure a very simple type of muscle is the only part that represents the neuromuscular mechanism of the higher animals. These muscles, moreover, are so insignificant in amount and so slight in their action that a living sponge seems more like a plant than an animal in its inertness. Compared with such sluggish responses as those shown by sponges, the movements of hydroids, coral animals, sea-anemones, jellyfish and other cœlenterates are quick, though the movements of these animals are in turn slow compared with those of vertebrates and especially of insects. This quickened rate of response, which distinguishes the cœlenterates from the sponges, is associated with the fact that the cœlenterates possess not only muscles but also nervous organs in the form of simple sensory surfaces by which their muscles are called into action more quickly than they would be by direct stimulation. Such a system includes two of the three elements already pointed out as essential to a complete neuromuscular organization and may be designated from the particular elements present a receptor-effector system.

The receptor-effector system with some of its most important modifications is well shown in such animals as

sea-anemones on which in fact some of the earliest studies in these directions were made. The more typical sea-anemones or actinians (Fig. 17) are cylindrical animals attached by one end, the pedal disc, to a rock or other firm support in the sea and carrying at the other end, the oral

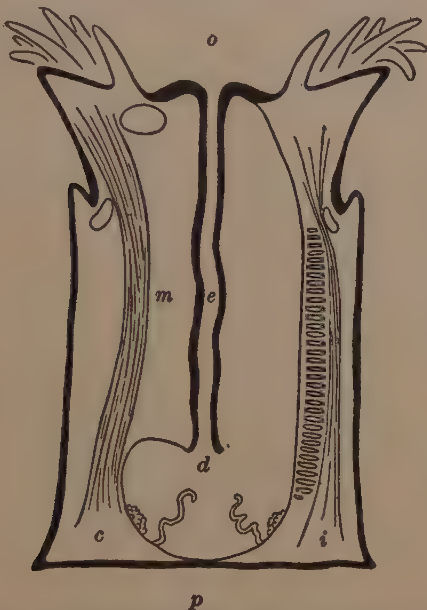


FIG. 17.—Diagram of a longitudinal section of the sea-anemone *Metridium*; the area of attachment is the pedal disc *p*; in the middle of the oral disc *o* is the mouth leading into the œsophagus *e* which opens into the digestive cavity *d*. The œsophagus is held in place by the mesenteries *m* when complete *c*, the incomplete mesenteries *i* failing to reach this tube.

disc, a cluster of tentacles in the center of which is the mouth. The mouth does not open directly into the single large internal space, the digestive cavity, but leads to a somewhat elongated œsophagus that extends downward into the interior of the actinian to the neighborhood of the pedal disc, where it opens out freely into the digestive cavity. The œsophagus, however, does not hang freely in the

digestive cavity, but is held in place by membranes, the mesenteries, which extend in pairs from the inner face of the cylindrical wall of the actinian's body, the column wall so-called, across the digestive space to the wall of the œsophagus. By means of these mesenteries the œsophagus thus comes to be held in an axial position in the actinian's body, where it serves as the one means of inlet and outlet for the digestive cavity. Although it is a relatively simple tube it is usually provided with a pair of longitudinal grooves, the siphonoglyphs (Fig. 18), by which water is continually passing into the interior of the sea-anemone to escape in an outward current through the rest of the œsophagus.

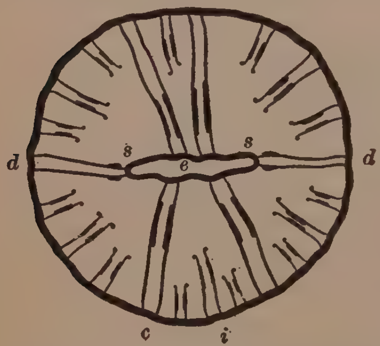


FIG. 18.—Transverse section of the sea-anemone *Metridium* showing the œsophagus *e* with its two siphonoglyphs *s* and its supporting mesenteries, the directives *d* and the complete non-directive *c*. Two series of incomplete mesenteries *i* are shown.

The mesenteries, as can best be seen in a transverse section of a sea-anemone (Fig. 18), are thin sheets of tissue which, as already mentioned, occur in pairs. The members of each pair are separated from each other only by a very narrow space, the entocele, which is really an extension of the digestive cavity. Each pair is separated from the pair on either side of it by a wider space, the exocele. The mesenteries that hold the œsophagus in place extend, as already stated, from that structure to the column wall and are known as complete mesenteries. Those that are attached to that portion of the œsophagus that forms a siphonoglyph have a peculiar arrangement

of muscles and are called directive mesenteries, the others being designated as non-directives. Besides the pairs of complete mesenteries, there are many other pairs of incomplete ones. These are characterized by the fact that they extend only a short distance into the digestive cavity and thus fail to reach the œsophagus.

The walls of a sea-anemone's body are in all places relatively thin. They are for the most part epithelial in nature and are composed of two layers of cells separated by a third layer of partly secreted, partly cellular material. Covering the whole exterior of the animal is the ectodermic layer, which at the mouth is reflected inward over the inner surface of the œsophagus to the inner termination of that tube. The whole interior of the sea-anemone is covered with the entodermic layer, which unites with the ectoderm at the inner end of the œsophagus. Between the ectoderm, which thus covers the exterior and the entoderm that lines the interior, is a third layer, the supporting lamella. As has already been stated this is composed of secreted substance containing numerous cells. It is resistent enough to give a good deal of support to the sea-anemone; hence it partakes of the nature of a skeleton. The body wall of the sea-anemone, as already mentioned, is everywhere relatively thin and wherever it is punctured the three layers mentioned are cut through, the ectoderm first, then the supporting lamella, and finally the entoderm, after which the digestive cavity is invaded.

The resolution of these layers of tissues into their cellular elements was first successfully accomplished by O. and R. Hertwig (1879-1880). Notwithstanding the differences in position and function of the ectoderm and entoderm, there is much uniformity in their neuromuscular

structure. The superficial portion of each is epithelial in character (Fig. 19) and contains among its various types of cells a number of sensory cells that terminate superficially in free, bristle-like endings and that branch at their deep ends into delicate fibrils. This epithelial portion may be designated as the first sublayer. The fibrils from the deep ends of the sense cells constitute collectively a nervous sheet, the second sublayer, in which may be found not only the deep terminations of the sense cells but also special elements, the so-called ganglion cells, whose branches add to the wealth of fine fibrils from the sense cells. Still deeper than the nervous layer is the muscular or third sublayer composed almost entirely of elongated muscle cells closely applied to the supporting lamella or even partly imbedded in it. These three sublayers can commonly be identified in many parts of the ectoderm and the entoderm.

FIG. 19. — Diagram of the ectoderm of a sea-anemone showing the epithelial *e*, the nervous *n*, and the muscular *m* sublayers.

According to the Hertwigs, when the sensory cells of a sea-anemone are stimulated, they transmit impulses to the nervous sublayer which in turn excites the muscles to action and thus the animal is brought to respond to an external change. If the stimulated sensory cells are in the ectoderm and the responding muscles are in the entoderm, it was supposed by these investigators that the nervous impulses pass through the ectodermic nervous sublayer over the exterior of the animal to the œsophagus, at whose inner end the impulses are transferred from the ectoderm to the entoderm and thus gain access to

the musculature of that layer. Although the Hertwigs believed that the nervous sublayer was rather uniformly developed all over the actinian, they maintained that a specially rich nervous region was to be found in the ectoderm of the oral disc, where the beginning of a central nervous organ might be said to occur. This view that the actinian possessed an oral concentration of nervous tissue was accepted by Wolff (1904), and by Grošelj (1909), who, however, placed the concentration in the wall of the œsophagus rather than in the oral disc.

Havet (1901), who studied the nervous system of the sea-anemone *Metridium* by means of the Golgi method, was unable to confirm the statement that the nervous elements were more abundant in the neighborhood of the mouth than elsewhere and declared that their arrangement was such as to justify the expression diffuse rather than centralized. Havet not only claimed a diffuse nervous system for actinians, but he maintained that there were grounds for changing in certain important particulars the scheme of nervous interaction proposed by the Hertwigs. According to Havet the so-called ganglion cells described by these authors are really motor nerve cells which receive impulses from the sensory cells and transmit them to the muscles. Thus the elements in the neuromuscular organization of an actinian form a sequence that reproduces in miniature that seen in the central nervous organs of the higher animals. Here, as, for instance, in the vertebrate spinal cord, a sensory neurone connects with a motor neurone which in turn leads to a muscle. The reflex arc thus outlined is reproduced in the actinian in that its sensory cell corresponds to the sensory neurone of the vertebrate and its motor nerve cell to the motor neurone. Thus the actinian and verte-

brate nervous system exhibit in one fundamental particular a most striking similarity.

Havet also claimed to have demonstrated a much closer relation between the ectodermic and entodermic nervous layers than was suspected by the Hertwigs. He believed that he could show by means of the Golgi method that nervous fibrils pass from the ectoderm through the supporting lamella to the muscles of the entoderm and thus establish a direct union between structures that, according to the Hertwigs, were only indirectly united through the œsophagus. This claim has been abundantly confirmed by Parker and Titus (1916), who have shown by a special technique for nervous tissue that the supporting lamella of the actinian *Metridium* contains an abundant meshwork of branching neurofibrils that can be traced from the ectodermic side of this layer through its substance to the more important systems of muscles in the mesenteries. Moreover, the supporting lamella can be seen to contain a great number of branching cells which have all the appearances of true nerve cells and which presumably form an essential part of the conducting system between the ectodermic sensory areas and the entodermic musculature.

These observations revive in a way the opinion early advanced by von Heider (1877, 1895) that the supporting lamella in a number of actinians contains nervous elements, a claim that, notwithstanding the opposition of Wolff (1904) and of Kassianow (1908), has been supported by the conditions found in the soft corals by Hickson (1895), by Ashworth (1899), and by Kükenthal and Broch (1911). Thus, though the details of the nervous organization in the actinians is only just beginning to be

worked out, the presence of nervous elements in these animals is beyond dispute.

The effector systems of sea-anemones, as might be expected, are more numerous and complicated than those in sponges. Sea-anemones possess at least four systems of effectors: mucous glands, ciliated epithelia, nematocysts, and muscles.

There has never been any ground for the assumption that the mucous glands and the cilia in cœlenterates are under nervous control. These effectors respond only to direct stimulation and are not open to influences from a distance. Even in the case of such cœlenterate cilia as those of the lips of actinians where by appropriate stimulation a reversal of the effective stroke can be brought about (Parker, 1896, 1905 *a*; Vignon, 1901), the whole reaction is so strictly local that there is not the least reason to assume the intervention of nerves. The mucous glands and cilia, therefore, bear all the marks of independent effectors and hence free from nervous control.

The nettle cells with their contained nematocysts, on the other hand, have often been regarded as subject to nervous influence. Schulze, who studied these cells in *Cordylophora* with great care in 1871, showed that each one was provided with a special bristle-like projection, a cnidocil, by which it could be stimulated directly, and argued from this that in their action they were independent of the nervous system. Nevertheless the discovery by the Hertwigs (1879-1880) that their basal processes branched as those of the sensory cells did, led these and many other investigators to believe that the nettle cells had nervous connections. This opinion has been expressed even as recently as 1913 by Baglioni. There is, however, not the least experimental ground for assum-

ing that nettle cells are discharged through nervous action. In the sea-anemone *Metridium* these cells are abundantly present on the tentacles and especially on those delicate filaments from the interior of this animal, the acontia. Nevertheless, from both these structures the nettling threads can be discharged only under direct stimulation and this continues to be true even after the part in question has been thoroughly and completely anesthetized with magnesium sulphate or chloretone. As these drugs temporarily abolish all traces of nervous activity and yet in no apparent way affect the activity of the nettled cells, it is most probable that these cells, like the mucous cells and the ciliated cells, are independent effectors and not under nervous influence (Parker, 1916 *a*).

Of the nervous control of the fourth type of effector in actinians, the muscle, there is abundant evidence. The muscles of these animals were regarded by the earlier workers as more or less continuous sheets that gave to the animal as a whole something of the character of a contractile sac. But after the publication of the important paper by the Hertwigs (1879–1880) on the structure of these animals, it became evident that their musculature was more differentiated than had been previously supposed and that a considerable number of well defined muscles or groups of muscle could be distinguished. These muscles, as already stated, occur in the deep portions of the ectoderm and the entoderm and may in some instances even invade the supporting lamella.

In *Metridium* it is possible to distinguish at least thirteen such sets of muscles. Their positions are indicated in Fig. 20. Of the thirteen only two are found in the ectoderm, the remaining eleven being in the entoderm. They

may be described briefly in the following order beginning with those in the ectoderm.

1. The longitudinal muscle of the tentacle is an elongated conical sheet of ectodermic fibers that are in direct

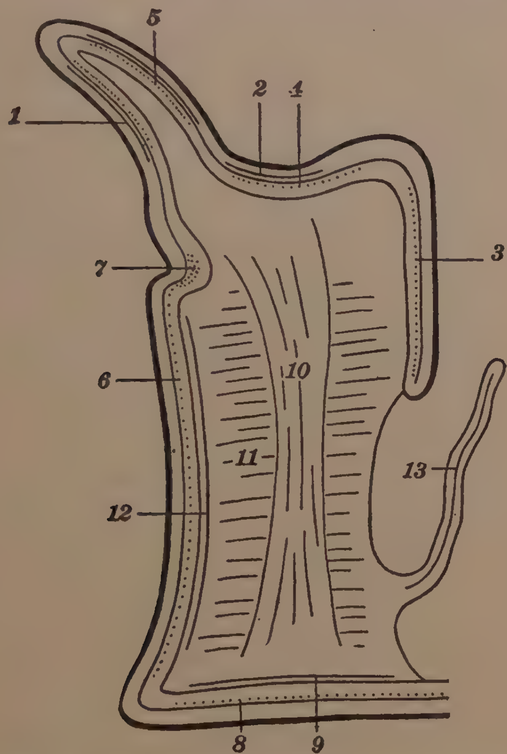


Fig. 20.—Diagram of a partial longitudinal section of the sea-anemone *Metridium* showing the thirteen classes of muscles: *1*, longitudinal muscle of the tentacle; *2*, radial muscle of the oral disc; *3*, circular muscle of the œsophagus; *4*, circular muscle of the oral disc; *5*, circular muscle of the tentacle; *6*, circular muscle of the column; *7*, sphincter; *8*, circular muscle of the pedal disc; *9*, basilar muscle; *10*, longitudinal muscle of the mesentery; *11*, transverse muscle of the mesentery; *12*, parietal muscle; *13*, longitudinal muscle of the acontium.

contact with the supporting lamella. They course lengthwise in the grooves and on the crest-like elevations that extend up and down the outer surface of the lamella, and

show no special grouping, being uniformly distributed around the whole tentacle.

2. The radial muscle of the oral disc is made up of irregular dense bundles of ectodermic fibers more or less imbedded in the supporting lamella of the disc. They radiate from the region of the mouth outward toward the periphery of the disc, making their way between the bases of the tentacles.

3. The circular muscle of the œsophagus ensheathes the œsophagus on its entodermic face. It is not very strongly developed and its fibers, which take a circular course, are more or less interrupted where the complete mesenteries are attached to the œsophageal wall.

4. The circular muscle of the oral disc is a flat circular ring, whose fibers take a course concentric with the mouth and are often much involved in the supporting lamella of the disc on its entodermic side.

5. The circular muscles of the tentacles are conical sheets of muscle on the entodermic side of the supporting lamella of those organs. In each muscle the fibers take a circular course and are fewer in number and finer than in the longitudinal muscle of the tentacle. They show no special differentiation except at the base of the tentacle, where there is a slight tendency to form a sphincter.

6. The circular muscle of the column is a well-developed sheet of cylindrical fibers covering the entodermic face of the supporting lamella of the column from its attachment to the pedal disc to the region of its transition to the oral disc. The fibers in their circular course pass the lines of attachment for the mesenteries at right angles, but are not to any great extent interrupted at these lines.

7. The sphincter is a firm circular band of muscle fibers embedded in the supporting lamella of the column

but so distributed that they show at once that they have been derived from an entodermic source. In fact, the sphincter is merely a differentiated part of the circular muscle of the column.

8. The circular muscle of the pedal disc is a well-developed, vigorous organ composed of a system of fibers concentric with the disc and more or less imbedded as circular bundles in the inner face of the supporting lamella of the disc.

9. The basilar muscles are radial strands that extend along the mesenteries at the junction of these organs with the pedal disc. There is a pair of these muscles for each mesentery and they vary in length in accordance with the size of the mesenteries to which they are attached. These muscles cross the fibers of the circular muscle of the pedal disc at right angles and lie only a very short distance orally from them.

10. The longitudinal muscles of the mesenteries are sheets of muscle fibers on the exocele faces of the directive mesenteries and on the endocele faces of the non-directives and of most of the incomplete mesenteries. They extend from the oral to the pedal disc.

11. The transverse muscles of the mesenteries are very thin uniform sheets of muscle that cover the endocele faces of the directives and the exocele faces of the other larger mesenteries. They are thus on faces opposite those on which the longitudinal muscles are located. They are better developed on the complete mesenteries than on the incomplete ones, from the smaller of which they may be entirely absent.

12. The parietal muscles of the mesenteries consist of longitudinal ridges on the exocele and endocele faces of almost all the mesenteries at their line of junction with

the column wall. On the larger mesenteries these muscles are small and inconspicuous in comparison with the other musculature of these organs, but on the very small mesenteries they are almost if not quite the only muscles present.

13. The longitudinal muscle of the acontium in *Metridium* is a delicate double band of fibers that extend lengthwise the filamentous acontium, one of which is attached to the free edge of each mesentery.

These thirteen sets of muscles constitute the effectors through which the nervous system of the actinians finds its only means of reacting on the surroundings, for the other three systems of effectors, the mucous glands, the cilia, and the nettle cells, are entirely free from nervous control.

CHAPTER VII

NERVOUS TRANSMISSION IN SEA-ANEMONES

A PLAN for nervous transmission in the body of a sea-anemone was long ago described by O. and R. Hertwig (1879-1880). According to this plan, it was believed that the stimulation of any given group of sensory cells on the surface of such an animal would excite activity in the subjacent nervous layer, which, in turn, would call forth contractions in the underlying muscles and thus originate a response. This is well exemplified in the tentacles of sea-anemones. When a strong stimulus is applied to the ectoderm of these organs they immediately respond by retracting due to a contraction of their longitudinal ectodermic muscles.

If, however, as is often the case, the sensory cells stimulated are in the ectoderm of the animal and the responding muscles are in its entoderm, the course of transmission as advocated by the Hertwigs was believed to be much less direct than in the former instance. In this case the nervous impulses that arose in the ectoderm were believed to be transmitted from their region of origin through the nervous layer of the ectoderm including the oral disc to that of the œsophagus at whose inner edge they passed over into the nervous layer of the entoderm by which they were conducted to the appropriate entodermic muscles. Thus the inner edge of the œsophagus was believed to be the region of nervous intercommunication between the ectoderm and the entoderm. Histological evidence that has led to the suspicion that this

view of the nervous connection of ectoderm with entoderm is not wholly correct has already been given in the preceding chapter, but much more conclusive physiological evidence to this effect will be presented here.

By appropriate lines of incision through the thin walls of sea-anemones it is possible to make preparations by which the courses taken by nervous impulses through the bodies of these animals can be determined with much accuracy (Parker, 1917 *a*). To test such preparations it is necessary to use a means of stimulation that is both accurately controllable and strictly local. Such a means is found in the mechanical stimulation produced by a delicate blunt glass rod. When the surface of a *Metridium* is explored by such means the degree of sensitiveness of the different regions is found to be as follows: Almost insensitive, the surfaces of the pedal disc, the lips, and the œsophagus; slightly sensitive, the surface of the column between the sphincter and the oral disc, the oral disc between the tentacles and the lips, and the siphonoglyphs; slightly more sensitive, the tentacles and the equatorial portion of the column; fairly sensitive, the surface of the column near the sphincter; and most sensitive, the surface of the column near its pedal margin. Stimulation of any of these regions was followed by a retraction of the oral disc due to a contraction of the longitudinal muscles of the mesenteries chiefly. The regions of stimulation, as the description implies, were always in the ectoderm; the response was made by entodermic muscles. Hence this particular set of reactions was very appropriate as a means of testing the course of nervous transmission from ectoderm to entoderm.

If the column wall of a sea-anemone is cut through in a complete ring equatorially, that is, if the column is gir-

dled (Fig. 21), a stimulus applied to the pedal edge of the column will call forth a contraction of the oral disc even more readily than when it is applied to the portion of the column that is on the oral side of the circular incision. Hence it must be admitted that there are transmission tracts that lead from the ectoderm of the pedal edge of the column directly through to the longitudinal muscles of the mesenteries irrespective of such connections as may exist in the œsophagus.

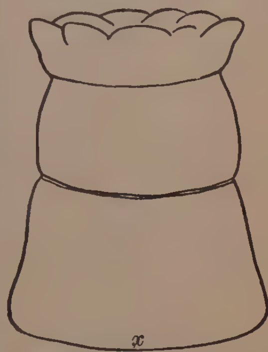


Fig. 21.—*Metridium* with its column wall completely girdled by a cut that passes at all points entirely through the wall. Stimulus applied at *x*.

The same conclusion can be drawn from what is seen in preparations from which the whole oral disc has been cut off. On stimulating the pedal edge of such a preparation the portions of the longitudinal muscles of the mesenteries still remaining in the animal contract vigorously, showing that there is not only a direct connection between the ectoderm of the pedal edge of the column and the longitudinal muscles of the mesenteries, but that the oral disc, believed by the Hertwigs to contain a centralized portion of the nervous system of the actinian, is in no way essential to the reaction noted. The belief that the oral disc does not contain an essential nervous center has already been vigorously set forth by Jordan (1908).

If the column of a large sea-anemone with a pedal disc 10 centimeters or more in diameter is cut through in an oblong outline, 4 centimeters by 2 centimeters, a superficial piece of the column results that is attached to the rest of the animal only through its mesenteries (Fig. 22).

Nevertheless, when the middle of this piece is stimulated mechanically or by discharging on it a small amount of hydrochloric acid in sea-water, a withdrawal of the whole oral disc follows. This response ceases when all the organic connections of the piece with the rest of the animal are severed by cutting through the attached mesenteries, thus allowing the piece simply to lie in place on the sea-anemone. The cessation of response under these circumstances shows that the transmission from the surface to the muscle must have been nervous and that it was not due either to the mechanical effects of the contraction of the piece itself on the deeper tissue, or to an accidental overflow of acid. Thus this experiment, like the two preceding ones, demonstrates a direct nervous connection between the ectodermic sensory apparatus of the column wall and the longitudinal muscles of the mesenteries.

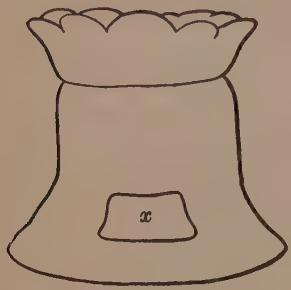


Fig. 22.—*Metridium* in whose column wall an oblong incision, 4 cm. by 2 cm., has been made so that the resulting piece is attached to the animal only by the mesenteries. Stimulus applied at x.

Fig. 23.—*Metridium* cut vertically in two except in the region of the lips. Stimulus applied at x.

If a sea-anemone is cut in two vertically in such a way that the resulting halves remain attached only by the lips (Fig. 23), not even the œsophagus or the oral disc remaining intact, and

if a mechanical stimulus is then applied to the column of one half, the portion of the oral disc in that half will be regularly withdrawn while that in the other half will be at most only rarely moved. Hence it follows that the region of the mouth, particularly of the lips, must be regarded as one poor in nervous connections. Consequently the view originally advocated by the Hertwigs and later by Wolff (1904) and by Grošelj (1909) to the effect that the region of the mouth is the chief region of nervous connection between the ectoderm and entoderm is not supported by direct observation, for, as has just been shown, this region is one poor in its capacity for nervous transmission and, as was shown earlier, there are abundant direct connections between the ectodermic receptors and the entodermic muscles without recourse to such areas as the region of the mouth and the œsophagus.

The conducting paths in the nervous organization of a sea-anemone can be demonstrated in a variety of ways. If a tongue of tissue is cut equatorially from the column of a sea-anemone so as to girdle it for half its circumference (Fig. 24), and a stimulus is applied to the free end of the tongue, such stimulus is only occasionally followed by a retraction of the disc, showing that this least sensitive portion of the column is not in

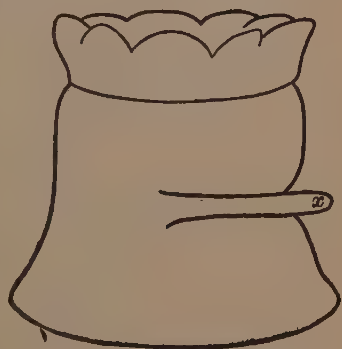


FIG. 24.—*Metridium* from which an equatorial tongue has been cut from the column. Stimulus applied at x.

what would be called free nervous communication horizontally with the rest of the column.

If, however, a tongue of the column wall is cut from the pedal edge of the column up to its equatorial region and there left in organic connection with the rest of the animal (Fig. 25) and a mechanical stimulus is applied to the free end of this tongue, a response of the whole system of longitudinal mesenteric muscles commonly follows.

FIG. 25.—*Metridium* from which a tongue running from the pedal disc to the equator of the column has been cut. Stimulus applied at x.

If a similar tongue is cut from the oral edge of the column down to its equator, a stimulus applied to the free end of this tongue will again call forth a retraction of the oral disc.

If the pedal edge of the column is cut off by an incision parallel to this edge and about 3 millimeters inside it, thus producing a band of tissue 4 to 5 centimeters long and attached by only one end to the animal (Fig. 26), a mechanical stimulus applied to the free end of this band is quickly followed by the retraction of the oral disc. If this band is anywhere completely cut across, a stimulus distal

FIG. 26.—*Metridium*, seen from the oral pole, from which a portion of the pedal edge of the column has been partly cut off. Stimulus applied at x.

to the cut is never followed by a retraction of the disc even though the two faces of the cut are in contact.

If a sea-anemone is cut through vertically except for its oral disc (Fig. 27), the mechanical stimulation of the column of one part is followed by a contraction of the longitudinal mesenteric muscles of both parts, thus dem-

FIG. 27.—*Metridium* cut through vertically except for its oral disc. Stimulus applied at x.

FIG. 28.—*Metridium* cut through vertically except for its aboral disc. Stimulus applied at x.

onstrating transverse nervous connections in the oral disc.

If the sea-anemone is cut through vertically as described in the preceding paragraph, except that the connecting portion is the pedal disc instead of the oral disc (Fig. 28), the stimulation of one part is followed by the retraction of the halves of the oral disc in both parts. Thus the pedal disc as well as the oral disc can serve the animal for transverse nervous connections.

Finally, if a sea-anemone is cut vertically in two, except for a small connecting bridge near the pedal edge of the column (Fig. 29), the mechanical stimulation of the column of one part is followed by a retraction of the halves of the oral disc in both parts.

These various tests and experiments show that the

longitudinal mesenteric muscles, by whose contraction the oral disc is depressed, may be called into action from almost any part of the outer surface of the sea-anemone. Paths of conduction must, therefore, exist between practically every point of the exterior of the animal and the longitudinal muscles of the mesenteries, and for these paths of conduction the oral disc and the œsophagus are in no way essential. In fact, definite and circumscribed paths appear not to exist, but, as the directions of the various incisions and cuts show, it is necessary to assume, first, an immediate connection between the superficial ectoderm and the deep-lying musculature, and, next, a veritable nervous network by which all manner of irregular and complicated incisions can be circumvented so long as a bridge of the natural tissue remains as a means of connection between the part stimulated and the part responding. In other words, some of the most characteristic reactions of sea-anemones are to be ascribed to the fact that these animals possess a well-differentiated nerve-net (Parker, 1917 *a*).

FIG. 29.—*Metridium*, seen from the oral pole, cut through vertically except for a small connecting bridge on the pedal edge of the column. Stimulus applied at *x*.

The location of this nerve-net is by no means clearly determined. At first thought it might be expected to occur in the nervous sublayer described in the ectoderm and in the entoderm by the Hertwigs. But doubt has already been expressed as to the nervous character of this layer (Parker, 1912). In *Metridium* the so-called nervous sub-

layer of the ectoderm is best developed in the region of the lips, but, as experimental studies have shown, this is precisely the part of the animal that is poorest in nervous conduction. It, therefore, seems probable that, though the so-called nervous sublayer of the Hertwigs must be penetrated by a host of neurofibrils from the overlying sensory epithelium, this sublayer must have some other function than that of nervous conduction, which must be carried out by another part of the animal. The part most probably concerned with nervous conduction, judging from the discoveries of the last few years, is the supporting lamella. This layer has long been known to contain a network of cells and from the work of Havet (1901) and of Parker and Titus (1916) the richness of its nervous connections can no longer be doubted. It would, therefore, not be surprising if future investigation should show that the chief mass of the actinian nerve-net should be found to be located in the supporting lamella and not in the so-called nervous sublayers of the ectoderm and the entoderm.

The rate at which the nerve-net of actinians transmits impulses has been determined for *Metridium* (Parker, 1918 *b*). When large specimens of this sea-anemone are prepared as shown in Fig. 26, and the stimulus is applied at the distal end of the tongue of tissue cut from the pedal edge, the longitudinal mesenteric muscles contract vigorously. If now the stimulus is applied to the root of the tongue, the muscular contraction occurs in less time than in the former instance. The difference between these two periods of time thus determined is the interval necessary for transmission between the two points stimulated. As the distance between these two points can be measured with accuracy, the rate of transmission can be easily de-

termined. At 21 degrees centigrade this proved to be from 121 millimeters to 146 millimeters a second, a relatively slow rate. In the particular form of preparation on which this determination was made, the tissue of the tongue exhibited no contraction during transmission, hence it is to be concluded that the type of transmission here measured was strictly nervous, and not muscular or a combination of nervous and muscular transmission.

The type of stimulation and response that has been described in the last few paragraphs for the sea-anemone is one of the most extensive and vigorous that this animal can carry out. If the stimulation is sharp and prolonged not only do the longitudinal mesenteric muscles continue to contract, but the tentacles shorten and contract, the circular muscle of the column aids in diminishing the volume of the animal, and, as the water from its interior is discharged, the sphincter, like a puckering string, draws the column over the retreating oral disc till the whole animal is changed from a beautifully expanded flower-like form to a shrivelled, contracted, and almost amorphous mass. In this extreme condition probably all the thirteen or more sets of muscles in the actinian's body have passed into a state of extreme contraction, which justifies more or less the older conception of the sea-anemone as a simple muscular sac. This state of contraction, a condition of extreme muscle tonus, may endure for hours or even days and illustrates well the chief characteristic of the musculature of many of these simple animals. In these forms the musculature is not adapted to the quick and varied movement that we associated with it in the higher animals, but it exhibits a condition of prolonged contraction, a state of extended tonus, such as is quite inconceivable in the skeletal muscles of a

vertebrate or an arthropod. In fact, the condition in the higher animals that seems most nearly to resemble this state of profound tonus in sea-anemones is that which follows strychnine poisoning or the poisoning from the bacillus of tetanus, a muscular spasm which, however, often results in death.

The recovery of a sea-anemone from this state of excessive muscular tonus is slow and gradual. It depends upon a reduction of the tonus, which exhibits itself in the form of a general relaxation of the musculature followed by a slow filling of the digestive cavity of the animal with seawater whereby it eventually assumes its distended form. This is carried out by the action of the ciliated siphonoglyphs through which currents of water are led into the interior of the animal. The process of recovery is, therefore, a relatively slow one as compared with the operation of contraction by which the water under rather high pressure is literally squirted from the animal's body.

Thus the character of this response illustrates well the nature of the nerve-net, for it shows that from any single spot on the surface of the actinian's body practically its whole musculature may be brought into excessive but normal contraction. Is it possible through this net to affect one set of muscles rather than another or is the net an open conducting system leading as freely in one direction as another? Theoretically such a diffuse condition has for some time been assumed, but it is questionable whether in even the simplest nerve-nets such an undifferentiated state really exists. The method of stimulation used in the preceding experiments, that by a fine glass rod, though apparently delicate, is in reality most harsh and unnatural as compared with normal stimuli for such ani-

mals. On applying such a rod to the pedal edge of the column of a sea-anemone the oral disc as a whole is depressed, an operation that involves the simultaneous action, as far as can be seen, of all the longitudinal muscles in the numerous complete and incomplete mesenteries of the animal. This means that scores and perhaps hundreds of these muscles act in unison. Is the nerve-net capable of only this gross form of activity or does it represent a system of finer gradations by which under an appropriate stimulus a part of this musculature can be excited to specific action while the rest remains essentially quiescent?

An answer to this question can be seen in the following experiment. If a *Metridium* is allowed to remain for some time in running seawater in a situation relatively dark, its muscular tonus will be reduced to a minimum and it will assume the condition of fullest normal expansion. If, under such circumstances, it is generally and briefly illuminated, it will quickly shorten its length quite noticeably though it will by no means go into what would be described as a state of contraction. This shortening of the animal as a whole is due to the simultaneous moderate contraction of its longitudinal mesenteric muscles. The fact that the shortening is symmetrical and uniform shows that a complete ring of these muscles have contracted in unison. If, instead of subjecting the fully expanded sea-anemone to a general illumination, light is thrown on only one of its sides, it responds usually by turning its oral disc toward the light, precisely as some flowers come to face the light. In the sea-anemone this is due to the contraction of those longitudinal mesenteric muscles that lie on the side illuminated, in consequence of which that side shortens and the oral disc is tilted in that direction. Thus

light, unlike the glass rod, can so stimulate the surface of an actinian that the subjacent nerve-net will call into action only that group of the longitudinal mesenteric muscles that lies close at hand and hence the nerve-net exhibits under a more normal form of stimulation a type of response much more delicate in character than what is seen when a glass rod is used. Probably these two types of responses are merely extremes of the same thing and differ only quantitatively; but, however this may be, they show quite clearly that if the mechanical stimulus from such a source as a glass rod could be sufficiently refined there is not the least reason to suppose that it could not be made to call forth as finely graded a response as light does. At all events the nerve-net under these circumstances does not appear to possess that property which is coming to be so commonly recognized in the nerve and muscle of the higher animals and which is exemplified under the head of the "all or none" principle.

CHAPTER VIII

JELLYFISHES

The cœlenterates whose neuromuscular organization has been most considerably studied are not the sea-anemones, but the jellyfishes. These animals belong either to the class *Hydrozoa* or *Scyphozoa*. The hydrozoan or craspedote jellyfishes are relatively small, even microscopic animals, characterized by the presence of a thin membrane, the veil, which extends from the edge of the bell partly across its open mouth. Because of their small size they are not very favorable for experimental work, and the best known from this standpoint are the larger forms, such as *Carmarina* and *Gonionemus*. The scyphozoan or acraspedote jellyfishes on the other hand are mostly large, sometimes very large, animals and consequently much more experimental work has been done on these than on the craspedote forms. They are characterized by a freely open bell without veil. They include such well-known representatives as *Pelagia, Cyanea, Aurelia, Cassiopea,* and *Rhizostoma.*

The neuromuscular system of a jellyfish is limited almost entirely to the edge and concave or subumbrellar surface of the bell. In *Aurelia,* for instance, the edge of the bell has upon it at regular intervals eight groups of sense organs, the marginal bodies. Each group includes an eye-spot, a static organ, and several other organs probably of the chemical sense. These receptors represent specialized and thickened portions of the superficial epithelium from which bands of nervous tissue spread cen-

trally over the subumbrellar surface to the region of the large circular sheet of muscle that forms a sphincter-like organ midway between the centrally located mouth and the edge of the bell. It is the contraction of this muscular band that reduces the cavity of the bell and, by thus driving the water out of this cavity, forces the animal forward. On the relaxation of this sphincter, the bell resumes its expanded form in consequence of the elastic action of its gelatinous tissue. The muscle fibers in the great majority of cœlenterates are like the smooth or non-striped variety in the higher animals, but the sphincters of jellyfishes are exceptional in this respect and are composed of cross-striped fibers. Not only are they thus structurally exceptional, but they are also unlike the ordinary cœlenterate muscle in that they are incapable of long-continued tonic contraction (Jordan, 1912) and in this respect they also resemble the cross-striped muscle of higher forms.

As already stated, each of the eight marginal bodies of *Aurelia* consists of a group of sense organs whose cells are a modified part of the superficial epithelium of the region. From the deep ends of these cells nervous prolongations reach out from the given sense organ toward the sphincter. The stretches of nervous tissue that thus emerge from each marginal body are made up not only of the basal prolongations of sense cells, but of many interpolated nerve cells whose form is usually that of a bipolar cell. In *Aurelia* these stretches of nervous tissue spread out almost at once on the plate-like sphincter, but in *Rhizostoma,* according to Hesse (1895), the nervous tissue from each of the eight marginal bodies forms a fairly well circumscribed band, which retains its radial course from near the periphery of the bell till it

reaches the much more centrally located sphincter. In the region of the sphincter of *Aurelia, Rhizostoma,* and other such jellyfishes, these nervous bands spread out diffusely over the whole muscle layer, producing thus a nervous layer more superficial in position than the muscle on which it rests.

The earlier workers were not able to state with certainty the mutual relations of the elements in this nervous layer. The prevailing opinion was that the layer was composed of bipolar nerve cells. Eimer (1878) described the processes from these cells as branched and stated that the branches from various cells united to form a network, a state of affairs that Schäfer (1879) was unable to confirm. Nor does the account of the nervous system of *Rhizostoma,* as given by Hesse (1895), lead to the conclusion that a true network is present. With improved histological technique Bethe (1903, 1909), however, showed that the nerve plexus spreading over the sphincter of *Rhizostoma* is a true nerve-net in which the processes from the various nerve cells are continuous. This nerve-net overspreads the surface of the sphincter as a network, in which the processes from the cell-bodies, though limited chiefly to a plane parallel with that of the sheet of muscle, are not all thus restricted, but in many cases may be traced, on the one hand, distally in among the surface epithelial cells and, on the other hand, proximally among the muscle cells. In respect to their directions the nerve processes are very unlike the underlying muscle fibers for while the nerve processes extend in a great variety of directions, the muscle fibers follow a most rigid arrangement and take a course circular in outline and concentric with that of the jellyfish as a whole. Thus on the outer surface of a very regularly arranged system

of muscle fibers is a diffuse and branching network of nerve cells.

A clear idea of the mutual relations of the epithelium, nerve-net, and muscle layer in such a jellyfish as *Rhizostoma* can be obtained from a section across its sphincter at right angles to the contained muscle fibers (Fig. 30). Such a section would of course have a radial position in the jellyfish as a whole. On its outer face is the layer of epithelial cells that covers the subumbrellar surface of the jellyfish. Next within is the nerve-net with its contained nerve cells and branching fibers, some of which can be traced in among the epithelial cells and others among the muscle fibers. Deepest of all is the band of muscle fibers of the sphincter muscle cut at right angles and penetrated more or less by nerve fibers from the nerve-net. This sequence of tissues from the outer surface inward is the same as that met with in sea-anemones, in which the epithelium is most superficial, the nerve-net next, and the muscles deepest. Although the conditions thus far described are chiefly those in the acraspedote medusæ, they reproduce in essentials the structure of the craspedote forms except in two particulars. In the craspedote jellyfishes there are no well-defined marginal bodies, but the sense organs of the edge of the bell are more diffuse in their arrangement. Further, the cras-

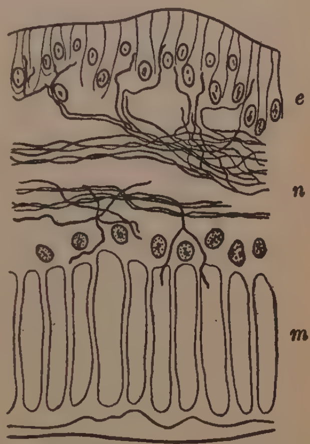


FIG. 30.—Section at right angles to the sphincter of the bell of *Rhizostoma;* the subumbrellar surface is uppermost; *e*, epithelium of the subumbrellar surface; *n*, nervous layer; *m*, muscle layer. (After Bethe, 1903.)

pedote medusæ, unlike those without the veil, are commonly characterized by a double band of nervous tissue encircling the margin of their bells. On the other hand, the subumbrellar nerve-nets and muscle bands are essentially alike in both the craspedote and the acraspedote forms.

The physiology of the neuromuscular mechanism of jellyfishes was independently investigated by Eimer and by Romanes. In 1873 Eimer presented before the Physikalisch-medicinische Gesellschaft in Würzburg a preliminary communication on his researches in this field, a published statement of which appeared in 1874, the year in which Romanes published his first brief note on the subject. Romanes' two extended papers appeared, one in 1877 and the other in 1878, the year in which Eimer's monograph came from press. The results of these two investigators were in essential agreement. In the main they entirely justified the view subsequently worked out by histological means that jellyfishes possess on their subumbrellar surfaces an intricate nerve-net.

It was found that if the eight marginal bodies of such a jellyfish as *Aurelia* were excised, the pulsations of the bell, for the time being at least, ceased. If all but one were excised, the pulsations continued and emanated from the one remaining marginal body. Such an animal formed a very convenient preparation on which to study the course taken by the impulse to contraction.

Both Romanes and Eimer showed that the bell of a jellyfish could be cut into a most complex pattern without interfering with the passage of the wave of contraction throughout its whole extent. If the single marginal body on a prepared bell of *Aurelia* is stimulated, a contraction appears in its immediate vicinity and spreads as two

waves, one to the right and the other to the left, around the bell till they fuse and become obliterated in a region opposite that from which they started. If such a bell is cut into a long spiral strip with the one remaining marginal body at one end and the center of the bell at the other, a wave of contraction can be started from the marginal body and will progress ordinarily over the whole

FIG. 31.—Diagram of the jellyfish *Aurelia* from which the central mass and seven of the eight marginal bodies have been removed. The outline of the bell has been further complicated by a system of interdigitated cuts. (After Romanes, 1893.)

length of the spiral. A much more complex preparation may be made by cutting out the center of a jellyfish bell, and then complicating it by a series of incomplete radial incisions in alternation, one set starting from the inner edge of the bell and the other from the outer edge (Fig. 31). A bell thus complicated by so intricate a series of interdigitations will nevertheless transmit a wave of contraction completely around its tortuous length. In fact, secondary interdigitations may be cut on the lines of any

of these primary cuts without necessarily interrupting the passage of the wave. Another extreme test may be carried out in which the jellyfish is reduced to two concentric rings attached to each other by only a small bridge of connecting tissue (Fig. 32). This type of preparation can be made by excising the center of a jellyfish and then

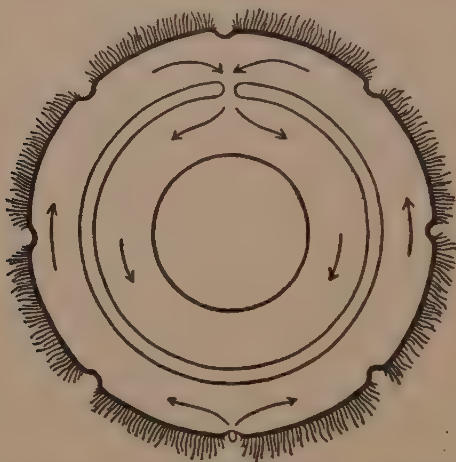


FIG. 32.—Diagram of the jellyfish *Aurelia* from which the central mass and seven of the eight marginal bodies have been removed. The outline of the bell has been further complicated by a circular incision that has nearly divided the bell into two rings. The arrows show the course of the contraction wave as it emerges from the one remaining marginal body and passes over the bell. (After Romanes, 1893.)

reducing it further by a circular cut parallel to its outer edge and midway between this edge and the center. The circular cut is so extended as to form a complete circle except for a fraction of an inch over which the outer ring is in organic connection with the inner one. When a wave of contraction is started from the one remaining marginal body on the outer ring, it will, on arriving at the bridge, pass across to the inner one irrespective of the region in the bell at which the bridge may be located, thus

demonstrating how small an amount of tissue is necessary for the transmission of a wave.

In *Cassiopea,* Mayer (1906, 1908) has shown that the two waves that emerge from the single marginal body are often of very different sizes. When two such disproportionate disturbances meet on the opposite side of the bell, the stronger wave commonly overcomes the weaker one and instead of having both disappear the stronger one continues its course around the bell. Such a wave once started may course indefinitely round and round a bell. This is particularly true if the bell has been so cut as to produce a very long circular stretch so that after the passage of the wave over a given portion of the stretch that portion has ample time to recover before the wave again passes over it. Harvey (1912) found that such a "trapped" wave may course over a circular path for as long as eleven days with no appreciable decline in rate. As this rate in *Cassiopea* averaged 46.472 millimeters per minute, the wave must have travelled in the eleven days somewhat over 457 miles.

As Eimer, Romanes, Mayer, and others have shown, jellyfish bells may be cut into patterns of the utmost diversity without, however, preventing the passage of their waves of contraction. As the majority of these patterns interrupt completely the course of the muscle fibers, but would always be circumvented by the nerve-net, it is generally assumed that transmission over the complicated outline to which the body of the jellyfish has been reduced must be dependent upon the nerve-net, not the muscles.

More conclusive evidence of the significance of the nerve-net in this respect, as contrasted with the muscle layer, has been obtained from several lines of work. Bethe (1903, 1909) has pointed out that in *Rhizostoma* the

sphincter muscle and the nerve-net are not coextensive. In *Aurelia* the sphincter forms a continuous circular band. In *Rhizostoma,* on the other hand, it is composed of a succession of sixteen muscle fields, a pair between each pair of the eight marginal bodies (Fig. 33). These muscle fields are partly separated from each other by areas of interven-

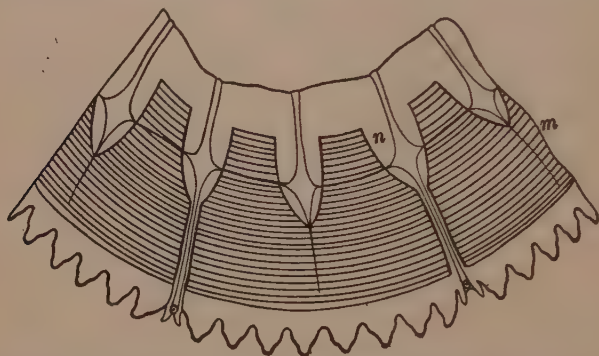


FIG. 33.—Diagram of a portion of the bell of *Rhizostoma* seen from the oral side; *m*, muscle field; *n*, area covered by the nerve-net but devoid of muscle. (Modified from Bethe, 1909.)

ing non-muscular tissue over which, however, the nerve-net extends. Consequently, it is possible to cut preparations from *Rhizostoma* in which one muscle field with an attached marginal body is connected with its neighbor only by an area of nerve-net (Fig. 34). When such a preparation is stimulated through its marginal body, not only does the immediately adjacent muscular field contract but also the more distant one. It is, therefore, clear that in this case transmission from one muscle field to the next is accomplished by the nerve-net and not by the muscle fibers.

Another piece of evidence bearing on this question has been advanced by Mayer (1906, 1908). *Cassiopea* is a jellyfish that possesses considerable powers of regenera-

tion. When the superficial tissue on its subumbrellar surface, epithelium, nerve-net, and muscle, is scraped off over a given area, the regenerative recovery is of such a kind that the epithelium and nerve-net appear soon and the muscle layer somewhat later. It is, therefore, possible to obtain in *Cassiopea* regenerating individuals in which the epithelium and nerve-net have been re-formed over the wound, but the muscles have not yet appeared. Such individuals may be cut into preparations in which two masses of muscle are connected only by a regenerated epithelium and nerve-net. When one muscle field in such a preparation is made to contract the other field also quickly contracts without the appearance of any movement in the intervening region. Hence it must be admitted that this intervening region, composed merely of epithelium and nerve-net, has the capacity of transmitting impulses to motion from one of the muscle fields to the other. This experiment, like that of Bethe, supports the belief that transmission over the subumbrellar surface of jellyfishes is accomplished by the nerve-net and not by the muscle.

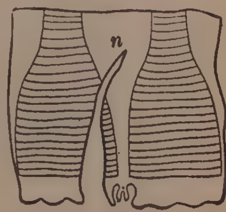


FIG. 34. — Preparation of two muscle fields from *Rhizostoma* to one of which a marginal body is attached; the preparation has been cut so that the second field is attached to the first, so far as its neuromuscular relations are concerned, only through the nerve-net, *n*.

The removal of all the marginal bodies from an acraspedote jellyfish is an effective way of rendering the bell at least for the time being motionless. The same kind of an operation can be carried out on a craspedote form by cutting off the edge of the bell. In such cases the edge usually carries with it some muscle tissue and will continue to pulsate for a long time, whereas the central por-

tion of the bell is quiescent. Loeb (1900) has shown that if the central portion of the bell of the craspedote medusa *Gonionemus* is thus rendered quiescent, its activity may be revived by placing it in a solution of ⅝ molecular sodium chloride, which is about isotonic with seawater. If to this solution a small amount of calcium chloride or potassium chloride is then added, the pulsations cease as in ordinary seawater, for the solution is thereby rendered a balanced one, as seawater naturally is, in that the stimulating effects of the sodium are counteracted by the calcium or the potassium.

Such a quiescent edgeless bell has upon its subumbrellar surface a nerve-net and a muscle layer. Whether in *Gonionemus* the sodium solution stimulates one or both of these has not been definitely determined, but in *Rhizostoma* a partial answer to this question has been found by Bethe (1909). When the eight marginal bodies of this jellyfish are removed, its bell is quiescent in ordinary seawater. Under such circumstances, however, it can be made to contract by stimulating it electrically or chemically. If now a preparation is cut from a *Rhizostoma* so as to include one marginal body and two muscle fields, the latter separated from each other by a partial cleft that allows the two lobes thus formed to be in physiological connection only through their nerve-net (Fig. 35), it is possible to determine the relative sensitiveness of the marginal body as compared with that of the rest of the neuromuscular mechanism. When in such a preparation the lobe without the marginal body is immersed in a 0.62 molecular solution of sodium chloride and the lobe with this body is in seawater, the rate of contraction of the whole preparation remains constant and normal. If, however, the lobe with the marginal body is now immersed in

the solution of sodium chloride and the other lobe is in seawater, the rate of contraction quickly increases to about three times what it formerly was. This shows that the particular concentration of sodium chloride used, 0.62 molecular, was stimulating for the marginal body but not for the nerve-net or the muscle. If a preparation that

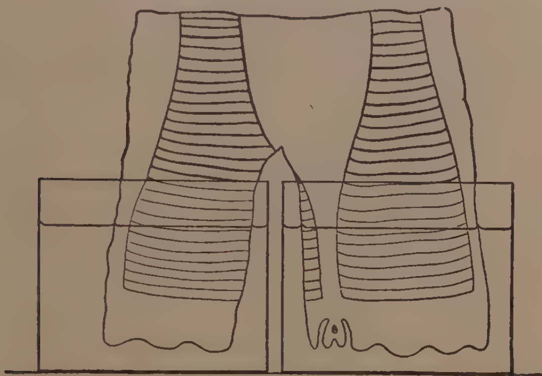


FIG. 35.—Diagram of a preparation of two muscle fields from *Rhizostoma*, one with an attached marginal body and the other without such a body and so arranged that the two fields may be partly immersed in vessels containing different solutions. Thus the sensitiveness of the marginal body may be compared with that of the rest of the neuromuscular structure. (Based on the description by Bethe, 1909.)

consists merely of nerve-net and muscle and that will not respond to a 0.62 to 0.66 molecular solution of sodium chloride, is now subjected to an 0.8 to full molecular solution of the same salt, contractions will reappear for a short time at least, showing that the combination of nerve-net and muscle, though not so sensitive as the marginal body, is nevertheless open to stimulation.

When a preparation in which there is only nerve-net and muscle is immersed in a sodium chloride solution, it is claimed by Bethe that both the region in which there is only nerve-net and that in which there is both nerve-net and muscle become more open to stimulation and that of

the two the region of the nerve-net alone is rendered relatively more sensitive than that composed of nerve-net and muscle. Bethe, therefore, concluded that, though the muscle may be open to direct stimulation, it is not so sensitive as the nerve-net and that consequently, when a portion of a *Rhizostoma* without a marginal body is made to contract, it probably does so through the action of the stimulating agent on the nerve-net rather than on the muscle. From this standpoint the neuromuscular mechanism of a jellyfish may be regarded as composed of three parts of graded susceptibility to stimulation: the marginal bodies, which are most sensitive and are stimulated by ordinary environmental changes; the nerve-net, which is less sensitive than the marginal bodies and is only rarely open to stimulation from the environment; and, finally, the muscle, which is the least sensitive of the three and is consequently only most rarely stimulated directly by environmental changes.

This contrast in the sensitivity of muscular and nervous components in the neuromuscular organization of the jellyfishes is quite in accord with what should be expected in the evolution of a receptor-effector system. The muscles of sponges are, in comparison with those in most other animals, extremely inert to stimulation and very sluggish in response. In this respect they are like the muscle of the cœlenterate divested of its nervous connections. It is only after such effectors as these have added to them receptors, such as are seen in the sensory surfaces of the sea-anemones or in the marginal bodies of the jellyfishes, that a quicker and more efficient system is established, whose improvement over the old one is dependent upon the increased sensitiveness of the new member, the receptor, rather than on any considerable change in the original member, the effector.

CHAPTER IX

THE NERVE-NET

The nerve-net of the lower animals contains the germ out of which has grown the central nervous systems of the higher forms. As a definite type of structure the nerve-net has been recognized only for a few years. Its discovery was brought about by the repeated attempts made since the declaration of the cell theory to resolve nervous tissue into its component cells. Although the cell theory as applied to animal tissues was enunciated by Schwann as early as 1839, it was not till more than half a century later that a clear and consistent idea of the nerve cell was arrived at.

Nerve fibers seem to have been first really seen and figured by the Florentine physician Felix Fontana in 1781, but it was not till 1833 that Ehrenberg in the preliminary announcement of a monumental work on the fibrous structure of the central nervous organs, described certain corpuscles that proved to be what later investigators called ganglion cells. The connection of these two elements, vaguely intimated in 1838 by Remak and surmised in 1840 by Hannover, was first really demonstrated for invertebrates in 1842 by Helmholtz and for vertebrates in 1844 by Kölliker, who showed that fibers with a medullary sheath, and therefore unquestionably nervous, were directly connected with ganglion cells. From the time of these discoveries, it became necessary to assume that in some way or other ganglion cells were integral parts of the nervous system.

In 1855 Leydig discovered in the ganglionic bodies of spiders what appeared to be a finely granular material which he called punctate substance. Similar material was also shown to be a considerable constituent of the gray matter of the vertebrate nervous system. Hence, in addition to nerve fibers and nerve cells, a third kind of material was shown to be present in many nervous organs. This material, as was subsequently demonstrated in 1871 by Gerlach, consisted in reality of very fine fibrils which when seen in section appeared as minute points and hence Leydig's name for it of punctate substance.

The uncertainty of the relation of this fibrillar material to nerve fibers and to nerve cells was not removed until the Golgi method of silver impregnation began to be generally applied to nervous tissues. This method yielded such important results that in May, 1891, Kölliker could substantiate the claim that every nerve fiber in the body was at some part of its course directly connected with a ganglion cell, and in June of the same year Waldeyer, on the basis of conclusions drawn largely from Golgi preparations, promulgated the theory of the neurone, the first consistent account of the nerve cell. According to this well-known doctrine the ganglion cell of the older workers is really the nucleated body of the true nerve cell, or neurone, whose processes are commonly of two kinds: fine protoplasmic processes from the cell body and nerve fibers with their final branchings. Both these kinds of processes may contribute to the formation of the finely fibrillar material already noted. This material was believed to be the means of intercommunication between neurones.

The embryological investigations of His (1886) and other workers showed that the embryonic nerve cells, or

neuroblasts, from which adult neurones were differentiated were in the beginning far separated from each other and only secondarily came together. Of their initial separation there could not be the least doubt; the question that arose concerned the extent of their final union. On both anatomical and physiological grounds there were good reasons advanced to show that, though the separate neurones came into such contact relations as was necessary for the transmission of nervous impulses, they never fused to such an extent as to lose their identities. The fibrillar material, in which these interrelations were known to occur, was, therefore, regarded, not as a continuous net, as Gerlach believed it to be, but as broken up into discrete neuronic systems separated one from another by an infinitude of minute interruptions, which, however, were capable of physiological continuity through what is known as a synapse. Thus each neurone, or true nerve cell, was believed to possess a certain amount of independence from its neighbors, though physiologically united to them at least by transmitting contact.

As the idea of the synaptic nervous system gradually unfolded itself to the more orthodox neurologists, there arose from another school of workers a very different conception of the interrelation of nervous elements. The impetus to this new movement came chiefly from the work of Apáthy, who in 1897 maintained on the basis of histological preparations of almost incredible clearness that the nervous elements of many animals were bound together by a network of neurofibrils in which there was not the least evidence of interruption such as is implied in the synapse. This view was in a way a revival of the idea of a continuous network as maintained in a previous generation by Gerlach. The careful reader of Apáthy's

papers will find it by no means easy to separate in them fact from speculation and, consequently, it is difficult to state in exact terms Apáthy's real contribution to this subject; but, however this may be, it is certainly true that the appearance of his publications excited others to a further investigation of the subject with the result that nerve-nets were proved to exist in a number of animals. As already stated, they were definitely identified by Bethe (1903) in jellyfishes, by Wolff (1904) and by Hadži (1909) in hydrozoans, and by Grošelj (1909) in sea-anemones. In fact, the cœlenterate nervous system seemed to be nothing but a nerve-net.

FIG. 36.—Nerve network from a small blood-vessel in the palate of the frog. (After Prentiss, 1904.)

Evidence was soon brought together to show that nerve-nets were at least components of the nervous systems of echinoderms, worms, arthropods, molluscs, and even vertebrates, where they were especially associated with the digestive tract and the circulatory system (Fig. 36), including the heart. Thus nerve-nets were identified from the cœlenterates to the vertebrates, and some of the more ardent advocates of this type of nervous organization went so far as to assume that it was the only type of nervous structure really extant and that the evidence of a synaptic system rested upon histological artefacts that obscured the real relations of cell to cell. But this extreme position has not been justified by further research. It is now generally admitted that the conceptions of a synaptic system and of a nerve-net are not opposing ideas, but represent two types of nerv-

ous organization, both of which may exist side by side in the same animal. Judging from the fact that the nerve-net is apparently the exclusive type of nervous organization in the cœlenterates and that it becomes progressively less and less evident the higher the animal series is ascended, it seems fair to conclude that the nerve-net is the more primitive type and that in the course of evolution it has given way more and more to the synaptic system which has finally come to be the dominating plan of nervous organization in the more complex animals. From this standpoint one of these animals might perfectly well possess both types of nervous structure; nerve-nets having been retained in its more conservative portions and synaptic structures having been developed in its more progressive parts. Thus the nerve-net may be regarded as phylogenetically older than the synaptic system. If the cell unit of the synaptic system is called the neurone, it would not be inappropriate to designate the more primitive units of the nerve-net as protoneurones (Parker, 1918 *a*).

Since the nervous system of the cœlenterates consists very largely of nerve-nets, the activities of these animals must reflect in a general way the peculiarities of this type of nervous organization. As the examples that have been given show, the nerve-net is almost always intimately associated with the muscles which it excites to action. Commonly the nerve-net is directly superimposed on the muscle layer or the two tissues may be more or less commingled. In either case the activity of the muscle may have a considerable influence on the state of the nerve-net, stretching it or squeezing it or in one way or another changing its physical condition. This relation has been made the basis of some important speculations

by von Uexküll (1909) as to the physiology of nerve-nets, namely that in transmission impulses flow more freely into regions where the net is stretched than into those where it is not. Attention will be called to examples of this kind in subsequent chapters.

As a result of the intimate relation usually existing between the nerve-net and the muscles that it controls, most organs that are provided with this type of neuro-muscular organization exhibit an extreme degree of autonomy. This is perhaps one of the most striking features associated with the nerve-net. It is well illustrated by such an organ as the tentacle of the sea-anemone, the autonomy of which was long ago recognized by von Heider (1879).

In most actinians the tentacles are hollow finger-like projections from the oral disc. Their cavities communicate freely with the common digestive cavity of the polyp and their walls consist of an outer layer of ectoderm separated by a supporting lamella from an inner layer of entoderm. In experimenting with tentacles it is desirable that they should be of large size, and this is the case in *Condylactis,* whose tentacles may be from 12 to 15 centimeters long and 1.5 centimeters in diameter. In this particular sea-anemone the tentacle terminates in a blunt end provided with a pore, and, as in the tentacle of *Metridium,* there are a longitudinal ectodermic muscle and a circular entodermic one.

If an expanded quiescent tentacle of *Condylactis* is touched near its tip with a silver sound or a glass rod, the tentacle contracts, usually bending toward the stimulated side. The tentacle often sticks to the object with which it is touched and it may in contracting thus exert a considerable pull, showing that its surface is remarkably adhesive and that its musculature is vigorous. If a

piece of crab meat or fish flesh is brought into contact with a tentacle, it adheres firmly to the tentacle which quickly shortens and is usually covered by several adjacent tentacles. The piece of flesh is thus held on the oral disc of the animal, which contracts in such a way as to move the mouth gradually toward the food till this aperture is near enough to swallow the flesh. The animal then slowly returns to a state of quiescent expansion.

When a tentacle of *Condylactis* is cut off and allowed to float in seawater, it contracts to about one-third its former length and remains almost indefinitely in this condition. Relaxation apparently never fully returns. If such a tentacle is caught on its cut edge by a delicate metal hook, it may be held with its open basal end at the surface of the seawater and inflated by gently running seawater into it. In this way a severed tentacle may be made to expand to about two-thirds its normal length and, under these circumstances, it will exhibit just about that degree of distension and mobility as is seen in the attached tentacles. If now, more seawater is discharged into it, it is likely to elongate a little and then contract considerably, discharging much of its contained water. Obviously for experimental purposes the fairly distended tentacle offers the most favorable condition.

Tentacles suspended in seawater and expanded to about two-thirds their natural length remain quiescent for considerable periods. From time to time, however, they show spontaneous movements consisting of slight contractions and twistings by which more or less of their contained fluid is discharged. If this is replaced, they will reëxpand and thus periods of quiescence are followed by periods of activity. In these respects the severed ten-

tacles reproduce very closely the behavior of the normally attached tentacles.

In response to slight or to vigorous mechanical stimuli the severed tentacles reproduce in a most striking way the movements of the attached ones under like stimulation. When an attached tentacle is gently touched on one side midway its length, the tentacle as a whole contracts but without much bending. If it is touched on the tip, the response is mostly a terminal waving back and forth. If it is stimulated on one side near the base, the contraction is chiefly basal and on the stimulated side. These responses are reproduced quite clearly by isolated tentacles. Thus the responses of the two classes of tentacles to localized stimuli are strikingly similar.

If a small amount of a 1 per cent. solution of acetic acid is discharged on an expanded severed tentacle, the tentacle contracts quickly with a curious appearance as though it were withering. After it has been washed with seawater, it may be distended again in about three to four minutes. A second and a third response have been elicited from such tentacles and these responses reproduce most strikingly the movements of attached tentacles. To a tenth per cent. solution of acetic acid both classes of tentacles show a slight local shortening. To a hundredth per cent. solution they respond by a slight curving. To a thousandth per cent. solution neither kind of tentacle shows any response whatever, as is also the case when pure seawater is discharged on them from a pipette.

To seawater discharged on the tentacles from a small pipette, no noticeable response is made by either class, but to seawater containing the juice from a crushed mussel, the attached tentacle exhibits active writhings often

accompanied by elongation. It is remarkable how strikingly similar to these are the responses of the isolated tentacles to the same juice. To a 1 per cent. solution of quinine hydrochloride in fresh water both classes of tentacles respond by quick contractions and often local constrictions.

In all the tentacular reactions studied the responses of the isolated tentacles agree most strikingly with those of the normally attached tentacles. Of course, the reactions of the isolated tentacles are not exact duplicates of those of the attached ones. They are feebler and less precise, but aside from differences such as these, which are quite clearly of an operative origin, the severed tentacle reproduces in a most striking way the responses of the attached tentacle (Parker, 1917 *b*).

The tentacles of *Metridium* are very small in comparison with those of *Condylactis* and in consequence detailed tests cannot be carried out on them with the ease and certainty that they can on larger forms. Nevertheless their general reactions are indicative of great autonomy. If the juices from fish flesh and other like food are discharged on the tentacles of an expanded *Metridium,* these organs will exhibit first a considerable amount of irregular movement and finally point toward the mouth, where in fact under ordinary conditions they would deliver the food itself. If, now, a tentacle is carefully cut off from *Metridium,* its original orientation in reference to the animal as a whole being kept in mind, the application of the stimulating juice will cause it, first, to undergo irregular movements and then to point in that direction that was originally toward the mouth. It is, therefore, evident that the tentacle of *Metridium,* like that of *Condylactis,* has within its own structure the neuro-

muscular mechanism necessary for carrying out a food response such as has been described (Parker, 1896).

This autonomy of organs is nowhere better illustrated than in the foot or pedal disc of the sea-anemones. Probably all actinians in which there is a well-differentiated pedal disc have some powers of locomotion. These are relatively slight and not often exercised in such a sea-anemone as *Metridium marginatum*, which is almost sessile; they are somewhat more evident in *Sagartia luciæ;* and they are decidedly characteristic of *Condylactis*. Pedal locomotion in all these forms is accomplished by a wave of contraction that arises on one side of the foot and sweeps slowly across it to the opposite side. Apparently this wave is not fixed in relation to the secondary axes of the animal. It may arise at any point on the periphery of the foot without reference to the internal organization of the animal, but, having once arisen it sweeps across the center of the foot so that a line drawn from the point of origin through the center of the pedal disc marks the direction of locomotion. In a specimen of *Condylactis* whose foot measured 13 centimeters by 8 centimeters, the passage of a locomotor wave required on the average 3 minutes and the animal progressed by means of each wave on the average a little over 1 centimeter (Parker, 1917 *c*).

To what extent are the creeping movements of the pedal disc dependent upon the animal as a whole? To answer this question experiments were carried out on *Sagartia luciæ*. Fully expanded, attached specimens of this actinian were suddenly cut transversely in two with a pair of sharp scissors. The oral pieces thus cut off and carrying with them in each case the whole of the oral disc, tentacles and so forth, were discarded. The attached pedal discs and remaining portions of the columns were

held under careful observation. These contracted at the level at which they had been cut so as to look like an actinian normally withdrawn. They soon filled themselves with water and, in twelve to fifteen hours after the operation, many of them were creeping about precisely as the whole animal did. A single record will illustrate this condition. One of the animals without its oral disc began creeping and was observed to carry out 4 movements in 16.5 minutes, travelling in that period a distance of 7 millimeters. An animal with its oral disc intact that had been kept under similar conditions as a control, carried out 4 locomotor movements in 22.5 minutes, travelling in that period 6 millimeters. As the differences between these two sets of records are no more than may be seen in any pair of normal individuals, the locomotion of the two animals may be regarded as essentially identical. Individuals without oral discs not only creep as whole individuals do, but they also attach themselves to a glass surface as firmly as do those with oral discs. Furthermore, those without oral discs creep away from the light as consistently as do normal individuals. In fact, so far as the creeping is concerned, it is impossible to distinguish one class from the other, except perhaps that the operated animals are somewhat less inclined to creep than the normal ones are.

These results are in entire accord with Loeb's investigations (1895, 1899) in which he has shown that an *Actinia equina* from which the oral end has been cut off, will creep more or less continuously on glass, and will attach itself firmly to a mussel shell just as a normal animal will. They are also in accord with Jordan's results (1908), in which it was shown that the reflex excitability and muscle tonus of actinians is not under the control of superior nervous centers lodged, for instance, in the

oral disc. They lead to the conclusion that the pedal disc and its immediately adjacent parts contain all the neuromuscular mechanism that is necessary to creeping; in other words, this function is in no sense dependent upon assumed nervous centers in other parts.

Thus the movements of the tentacles and of the pedal discs of actinians, parts whose nervous organization is that of the nerve-net, exhibit in a striking way an unusual degree of autonomy, and in this respect these organs are in strong contrast with such parts as the appendages of arthropods or of vertebrates whose activities are dependent upon a centralized nervous system and not a nerve-net, and disappear almost completely when they are severed from that part of the body in which the central organ is located. Thus the autonomy conferred by a nerve-net upon a given organ is one of the striking features of this type of organization as compared with that seen in animals with centralized systems.

Autonomy is characteristic not only of cœlenterate organs in which there are nerve-nets, but also of those parts of the higher animals in which there are similar structural conditions. The pedicellariæ, spines, and ambulacral feet of the echinoderms very probably belong under this head as well as the remarkable cloacal organ of holothurians whose pulsations have recently been studied by Crozier (1916). Autonomous organs with their nerve-nets seem to be less in evidence in worms and in arthropods than in the lower animals. In mollusks the foot is apparently largely autonomous and provided with a nerve-net, and the labial palps of the bivalve *Anodonta* are in this respect truly remarkable (Cobb, 1918). In vertebrates nerve-nets are abundantly present in connection with the circulatory system. The adult verte-

brate heart is a muscle freely permeated by a nerve-net. It has already been pointed out that there is a sharply marked difference of opinion as to the nature of the heart's contraction, some investigators maintaining that the beat is dependent upon a rhythmic activity of the nervous tissue that is transferred to the muscle; others, and these include the majority of modern workers, that the rhythm originates in the muscle itself, the nerve-net and other such structures being merely means of modifying the beat. Strong evidence in favor of the latter or myogenic theory of the heart-beat is found in the fact that the heart of the vertebrate embryo beats long before the first appearance of nervous tissue and that in tissue cultures single rhythmically contractile muscles fibers beyond the reach of anything possibly nervous can often be found. Yet, notwithstanding this evidence, it is entirely possible that the cardiac nerve-net may have come to be a more intimate part of the rhythmic mechanism of the adult heart than is supposed by many, in which case this organ in its autonomy would have a strong resemblance to the actinian tentacle, for, like the tentacle, it may be removed from the animal and by appropriate means made to act in a strikingly normal manner for a relatively long time.

Another portion of the vertebrate body that exhibits much autonomy and at the same time possesses a nerve-net is the digestive tube; especially the small intestine. Under normal circumstances the food in the small intestine is carried along from the end next the stomach to the outlet into the large intestine by a process of peristalsis, the essential part of which consists of a wave of constriction that starts in the higher part of the tube and passes downward to its lower end. This wave of constriction is preceded by a wave of relaxation which nat-

urally facilitates the progress of the food. Besides peristalsis the small intestine exhibits what has been called rhythmic segmentation. This consists of a set of constrictions whereby a continuous band of food is broken up into a series of masses like a string of beads. Each mass is then subdivided into two by a new constriction and the two halves from adjacent masses fuse to form a new mass. By a repetition of this process the food becomes completely mixed with the digestive secretions and is brought abundantly in contact with the absorbing intestinal walls.

FIG. 37.—Diagram of the nervous organization in the intestinal wall of a vertebrate (after Lewis, 1910); *m*, mucous layer; *s p*, submucous plexus; *c m*, circular muscle; *m p*, myenteric plexus; *l m*, longitudinal muscle; *s*, serous layer.

The walls that carry out these movements (Fig. 37) consist of a mucous epithelium on the inside followed by a submucous layer containing the submucous or Meissner's nerve plexus. This is followed in order by the layer of circular muscle fibers, the myenteric or Auerbach nerve plexus, and the layer of longitudinal muscle fibers, that abuts against the serous layer. In both the submucous and the myenteric plexus the cells present all the characteristics of protoneurones and form a continuous network; these two plexuses may therefore be regarded as true nerve-nets. In addition to this intrinsic nervous mechanism the small intestine receives nerve fibers from the vagi and the sympathetic chain.

If these extrinsic nerves for a given part of the small intestine are cut, that part will still exhibit rhythmic con-

tractions. In fact, Mall (1896 *a*) has shown that a piece of small intestine may be removed from the body, kept on ice twenty-four hours, and on being perfused in a warm bath, will contract rhythmically, an observation confirmed in its essentials by Cannon and Burket (1913). The small intestine must, therefore, be admitted to exhibit a high degree of autonomy. Magnus (1904) has attempted to obtain evidence as to the location of the layer or layers concerned with this autonomy. If a piece of intestinal wall is split so as to remove the mucosa and submucosa with the submucous plexus, the remaining portion will exhibit all the reactions that the section of the intestine before the removal showed. Hence it is believed that the submucous plexus is not necessary for the essential movements of the intestines. If, now, the remaining portion is separated into two sheets, one including the circular muscles and the other the myenteric plexus and the longitudinal muscles, that containing the circular muscles shows no response except to mechanical stretching while the portion containing the myenteric plexus and the longitudinal muscles will still exhibit spontaneous rhythmic movements. It, therefore, seems probable that the movements of the small intestine depend largely upon the myenteric plexus and that this plexus represents a nerve-net that acts on the adjacent musculature much as the nerve-nets in the lower animals do. In this way the small intestine, though under the influence of extrinsic nerves, also retains a relatively high degree of autonomy dependent upon its nerve-net. Its activities, particularly its rhythmic segmentation, affords an excellent example of von Uexküll's principle, for the segment of the intestine that is momentarily distended, whereby its nerve-net is stretched, is the region into which the impulses for renewed contraction flow most freely.

CHAPTER X

TRANSMISSION IN THE NERVE-NET

A SECOND peculiarity commonly attributed to the nerve-net as contrasted with the synaptic nervous system is diffuse transmission. In the synaptic nervous system of the higher animals nervous impulses travel from the receptors in one direction only, over well-circumscribed paths to given effectors; in other words, the synaptic nervous system exhibits a high degree of polarity. In the nerve-net, on the other hand, an impulse started at any point is believed to spread freely in all possible directions throughout the structure. This aspect of the nerve-net is best seen perhaps in the subumbrellar system of the medusæ. As Romanes (1877, 1878), Eimer (1878), and especially Mayer (1906) have shown, this net may be cut into the most intricate patterns and yet so long as the original organic continuity from point to point exists a nervous impulse may be started anywhere and will spread throughout the full extent of the tissue. Much the same form of diffuse transmission is to be seen in the sea-anemones, from almost any point of whose surface the whole retractor musculature may be brought into action.

In other examples of the nerve-net evidences of beginning polarization can be seen and these may be regarded as suggestive of the kind of steps by which the nerve-net was converted into the synaptic system. This is perhaps nowhere better seen than in the tentacles of actinians. When the tip of a tentacle is vigorously stimu-

lated, the whole tentacle is likely to respond, but when a point lower down on the side of the tentacle is stimulated, the reaction is chiefly from this point proximally; in other words, transmission is more readily accomplished from the tip toward the base of the tentacle than in the reverse direction. The same kind of evidence has been shown by Rand (1909) to come from the reparative steps in regeneration. If a tentacle is cut off, the stump contracts vigorously and on reëxpanding forms a terminal nipple; the cut face of the distal segment usually contracts only a little and seldom, if ever, closes the open wound. Yet, if such a distal piece is again cut crosswise, its proximal part contracts and eventually forms a nipple, while the distal piece remains almost unaffected (Fig. 38). The polarity thus exhibited is in the same direction as that which was shown by the reactions of the attached tentacle to mechanical stimulation.

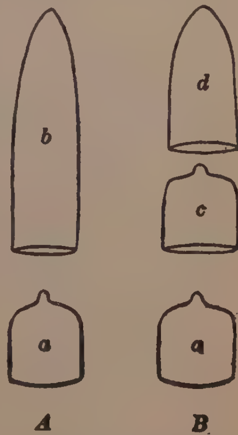


FIG. 38.—Diagram of the reactions of a tentacle of a sea-anemone to transection. On transecting a tentacle *A*, the distal end of the proximal piece *a* contracts and forms a nipple and the proximal end of the distal piece *b* remains open. On transecting the distal piece *B* the process is repeated in that the distal end of the new proximal piece *c* forms a nipple and the proximal end of the new distal piece *d* remains open.

If the tentacles of a sea-anemone that has been thoroughly anesthetized with chloretone are touched, no response whatever follows. If they are cut, neither the proximal nor the distal parts contract but both remain flabbily open. In consequence of these conditions it is believed that the polarity of the tentacle in so far as it is exhibited by the reaction just noted is of a nervous na-

ture, for it disappears on applying a drug that eliminates nervous activity (Parker, 1917 *b*).

When the nervous structure in the tentacle of an actinian is examined with the view of seeking some condition upon which this form of polarity can be based, a most simple relation is discoverable. As Grošelj (1909) has pointed out, the nerve fibrils that arise from the sense cells in the tentacles of actinians extend as a rule in a direction corresponding with the length of the tentacle. In *Bunōdes* many of these cells are bipolar and in that case one fibril extends distally along the tentacle and the other proximally, but there are also in this actinian a goodly number of cells that are unipolar and in such instances the fibrils almost invariably extend toward the base of the tentacle. In *Cerianthus* (Fig. 39) almost all the sense cells in the tentacular ectoderm are unipolar and their fibrils run almost without exception toward the base of the tentacle. As these fibrils transmit impulses away from the receptive cell bodies with which they are associated, it follows that in both these actinians nervous transmission must be predominately toward the base of the tentacle and that consequently the region of response would be largely proximal to the region of stimulation. This is what is to be seen in the neuromuscular reactions of most actinian tentacles and it is, therefore, believed

FIG. 39.—Sense cells with their attached fibers in a tentacle of the sea-anemone *Cerianthus*. The arrow points toward the base of the tentacle, a direction taken by most of the fibers. (After Grošelj, 1909.)

that the polarity of these organs, as evidenced in the processes just mentioned, is dependent upon the proximal direction taken by the sensory fibrils in these structures whereby the nervous impulses are led to flow predominantly toward the base of the tentacle. This anatomical interpretation of the polarity of the tentacle is supported by the observation made by Chester (1912) that after two tentacles of *Metridium* have been grafted together base to base there is no change in their neuromuscular polarity.

Signs of polarization occur not only in the nerve-nets of the lower animals, but they are also evident in those of the higher forms. The rhythmic segmentation of the small intestine, already mentioned, may at times be a purely local process unconcerned with the progress of the food. Under such conditions the intestinal nerve-net must be acting as a diffuse mechanism. Commonly, however, segmentation is associated with peristalsis and the food is not only churned but moved along through the intestine. The direction of this motion is regularly toward the anus and the polarity thus exhibited is not unlike that seen in the actinian tentacle. That intestinal polarity, like tentacular polarity, probably rests on a structural basis is seen from an experiment by Mall (1896 *b*) in which a section of small intestine was cut free, turned end for end and healed into its old position reversed (Fig. 40). After recovery the animals began to show serious digestive complications, and on killing and examining them it was found that the food had accumulated in the intestine at the stomach end of the reversed piece, a state of affairs indicative of marked and persistent polarity in the intestinal nerve-net.

The heart of the lower vertebrates also exhibits pro-

nounced polarity, for contraction normally begins in the region of the sinus and progresses thence in sequence over the auricle, the ventricle and the bulb. The fact that by appropriate stimulation this sequence may be reversed gives the heart a more diffuse character than the small intestine shows. But the uncertainty as to the myogenic or neurogenic nature of its beat leaves the heart a less clear example of these peculiarities than some other instances.

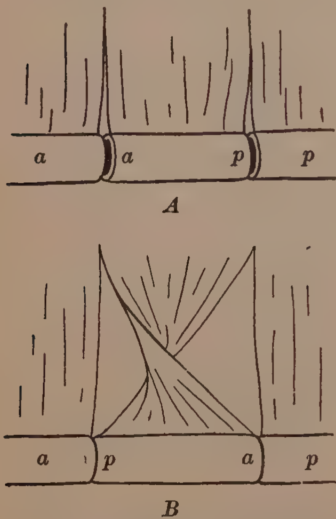


FIG. 40.—Diagram to illustrate the preparation of the intestine in Mall's experiment on intestinal polarization. *A*, piece of intestine suspended by its mesentery and freed by two transections, but still in normal position. *B*, the same, but with the piece of intestine healed into place in reversed position. *a*, anterior; *p*, posterior.

As diffuse transmission is characteristic of the nerve-net and polarized transmission is a feature of the synaptic system, it follows that the first signs of polarization in the nerve-net may be regarded as the initial step in the process of converting this organ into one of a synaptic type. As this process is apparently accomplished by the elongation of the neurofibril constituents of the net in a particular direction, this feature may be regarded as the anatomical indication of the coming change. With the growth of such a feature the nerve-net begins to lose its diffuse condition and its transmitting fibrils come to form bands or trunks with some resemblance to nerves; in other words, the nerve-net loses some of its net-like character and comes to develop a partial

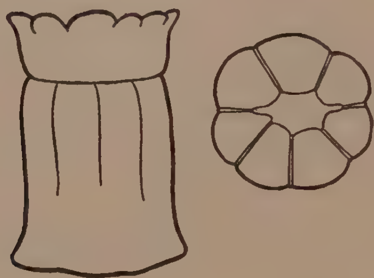
cleavage or grain. Consequently receptive cells, instead of being closely associated with the muscles that they control, may come to lie at some distance from them and thus arises the necessity for extended transmission. This is clearly seen in the contrast between the tentacles and the general retractor mechanism of actinians. In the tentacles a system of ectodermic sense cells immediately overlies the ectodermic longitudinal muscle and hence conduction from the sense cells to the muscle is simple and direct. In the retractor mechanism, on the other hand, an ectodermic system of sense cells calls into action a distant entodermic system of retractor muscles in the mesenteries, and this involves not only a nerve-net but a net of such dimensions as to accomplish the extended transmission necessary for the performance of general retraction.

Such modifications of the nerve-net lead to conditions in which are realized the beginnings of unquestionable reflex activity. In this form of response a definite motor or other efferent activity appears after the application of a specific stimulation. In other words, on the application of a definite stimulus not a diffuse response but a highly particularized one appears. This is well seen in certain reactions that depend upon oral and tentacular stimulation in the sea-anemone *Metridium*.

If a small amount of seawater is discharged into the mouth of an expanded, resting *Metridium*, no response is usually noticeable. If the seawater contains hydrochloric acid $\frac{n}{20}$, the actinian immediately opens the œsophagus widely and exhibits on its column a few well-marked vertical grooves. These disappear gradually as the œsophagus closes. If the position of these grooves is carefully noted, it will be found that one is always present for each siphonoglyph and that the others are distributed in ac-

cordance with the arrangement of the other pairs of complete mesenteries (Fig. 41). The grooves thus mark the lines of attachment of these mesenteries and are the result of the contraction of their transverse muscles, which are those concerned with the opening of the œsophagus.

If fragments of fish meat are put on the lips of a fully expanded *Metridium*, they are carried into the animal by



A B

FIG. 41.—*A*, outline of the sea-anemone *Metridium* showing on its column the vertica grooves that accompany the opening of the œsophagus. *B*, transverse section of the same sea-anemone to show the relation of the œsophagus and grooves to the pairs of complete mesenteries whose transverse muscles open the œsophagus and form the grooves.

ciliary action through an œsophagus that opens widely to receive them and during this operation the column of the animal is marked by the same vertical grooves that were seen in the experiment with acidulated seawater. As the pieces of food pass into the digestive cavity the grooves fade out. It is clear, then, that the transverse muscles of the complete mesenteries are concerned with the expansion of the œsophagus for the reception of food.

If a piece of fish meat is placed upon the tentacles of an expanded *Metridium*, these organs become characteristically stimulated and if the meat is removed before it is brought by the tentacles to the animal's lips, the œsoph-

agus will still open, accompanied by the formation of vertical grooves on the column. This response can not be elicited by the application of weak acid to the tentacles. Under such circumstances a withdrawal of the oral disc takes place. Thus it appears that not every form of effective chemical stimulus that can be applied to the tentacles is followed by an opening of the œsophagus. To appropriate stimuli, however, the tentacles and lips may act as receptors for the opening of this tube. No other parts of the body of *Metridium* have been found from which this œsophageal response can be called forth. The response, therefore, partakes of the nature of a true reflex in that it implies definite transmission tracts from the tentacles and from the lips to the transverse muscles of the mesenteries, and these tracts are called into activity only by specific forms of stimulation. Thus while dilute acid applied to the tentacles will excite the general nerve-net of *Metridium*, fish meat applied to these organs calls forth the œsophageal response only. Jordan (1908) has claimed that animals possessing only nerve-nets in their nervous organization exhibit reflex deficiency and this in general is undoubtedly true, but, as the present example shows, some of these animals may have involved in their nerve-nets specialized tracts that enable them to carry out simple but obvious reflexes. Such conditions indicate the steps by which a nerve-net may be converted into that type of central nervous organ that is characteristic of the higher animals (Parker, 1916 *a*, 1917 *d*).

CHAPTER XI

APPROPRIATION OF FOOD AND THE NERVE-NET

If the cœlenterates, whose nervous system is largely a nerve-net, nevertheless exhibit locally signs of a higher differentiation, may it not be possible that in some of their more complex operations they may show signs of all the higher nervous functions of the most complex animals? In attempting to find an answer to this question, so far as actinians are concerned, such activities as their feeding habits, their retraction and expansion, and their locomotion have been investigated.

The appropriation of food is an activity with which the oral disc of actinians is principally concerned. The movements of the tentacles, mouth, and other such parts by which food is ingested were ascribed by Nagel (1892, 1894) to muscular action alone, but Loeb (1895) pointed out that cilia also play an important rôle. The parts that are immediately concerned in the appropriation of food are the five following: the tentacular gland cells, whose secretions render the tentacles adhesive, whereby pieces of food become attached to them; the musculature of the tentacles, by which these organs are pointed toward the mouth; the tentacular cilia, which sweep toward the ends of the tentacles and thus deliver the food to the mouth when the tentacles are pointed in that direction; the transverse muscles of the complete mesenteries, by which the œsophagus is opened; and the cilia of the lips and œsophagus, which in the presence of food reverse their

usual outward stroke and thus transport such materials to the digestive cavity. Besides these five sets of parts some actinians include in the means by which they appropriate their food a sixth system, namely, the musculature of the oral disc. In *Stoichactis,* for instance, as described by Jennings (1905), and in *Cribrina,* as reported on by Gee (1913), the mouth during feeding is moved by the oral musculature toward the food-bearing tentacles, a shifting which has also been observed in certain corals (Carpenter, 1910). This operation, though it can be seen to occur in *Metridium,* is relatively so insignificant in this form that it may be passed over without comment; the important elements in the feeding of this actinian are the five already mentioned.

Much confusion and uncertainty exists in the various accounts of the methods by which actinians obtain their food and more or less of this is due to the failure on the part of writers to designate the particular form of activity that they are for the moment discussing. Thus both ciliary and muscular activity are involved in the appropriation of food and have often been indiscriminately dealt with in accounts of this operation. Their significance for the animal as a whole is, however, very different and it is, therefore, highly desirable that they should be kept clearly in mind as separate processes in any discussion in which they are involved.

Of the five principal events that go to make up the act of food appropriation, three exhibit so little variation that they may be regarded as essentially uniform. These are the secretion of mucus, the beat of the tentacular cilia, and the opening of the œsophagus. In none of these are there during feeding any important readjustments which

are essential to the acquisition of food; the production of mucus is apparently a strictly local response to a local stimulus; the beat of the tentacular cilia is constant and irreversible; and the opening of the œsophagus is as simple and mechanical a reflex as can well be imagined. The idea that the œsophagus, as often intimated, exhibits peristalsis is probably incorrect. At least a careful inspection of this organ in action in *Metridium* gives no support to this idea. The two remaining events in the appropriation of food, the responses of the oral cilia and the movements of the tentacles, are both open to significant changes and are of the utmost importance in judging of the relation of this process to the actinian as a whole.

Unlike the tentacular cilia, the oral cilia, those of the lips and of the œsophagus, may reverse the direction of their stroke so that the usual outward current can be converted into an inward one. This reversal is, under ordinary circumstances, a local response on the part of the cilia to certain dissolved substances in the food. Its relative independence of the other activities of *Metridium* can be shown in a number of ways. Thus, though it is a response to food, excessive feeding has no marked influence on it. Allabach (1905) caused a *Metridium* to gorge itself with food, a process that can result finally in disgorgement, and yet immediately after the animal had emptied itself, its oral cilia were found to reverse to food, which was thus passed down its œsophagus. Further, if pieces of meat are fed to the lips of the oral half of a *Metridium* cut transversely in two, the cilia reverse and the masses of food thus carried through the œsophagus are discharged at its open pedal end. By this means in the course of an hour or so many times the amount of food

that the body of a *Metridium* could contain can be passed through its œsophagus, and yet the ciliary reversal is as effective after this period of continuous feeding as before.

Other evidence of the relative independence of the oral cilia as compared with other effectors is well seen in specimens of *Metridium* that have been narcotized with chloretone, by which all nervous activity is abolished. A piece of food placed upon the tentacles of such an animal calls forth no special response and either remains where it was placed or moves sluggishly off to the periphery of the disc under the action of the tentacular cilia. When, however, such a piece is put on the lips, the cilia reverse and the morsel is gradually carried down the œsophagus and discharged into the digestive cavity. The swallowing is usually not so rapid as in the normal animal, for, under this form of narcotization, the transverse muscles of the mesenteries do not respond to the food by opening the œsophagus and consequently the cilia are obliged not only to transport the morsel but to force it down a partly closed tube. This, however, they are usually able to do, and thus, quite independent of neuromuscular help, they bring about the swallowing of food and the rejection of non-food, for under these circumstances inert materials were found not to reverse the ciliary stroke. Thus, as Allabach (1905) has pointed out, the reversal of the effective stroke of the oral cilia is a process that is largely independent of the physiological state of *Metridium*.

In one particular only does this process appear to be related to the general condition of the animal. Ordinarily the reversal of the oral cilia is accomplished by dissolved substances from the food, and in the earlier studies on this subject in *Metridium* this was believed to be the only way by which such reversal could be induced

(Parker, 1896). Torrey (1904 *a*), however, showed that in *Sagartia* this reversal could be brought about by mechanical stimuli as well as by chemical means and that it was favored by a starved condition of the animal. Allabach (1905) also found that in *Metridium* a ciliary reversal could be induced by mechanical means, and Gee (1913) has recently shown that specimens of *Cribrina* which have been in the laboratory some time do not exhibit a reversal to mechanical stimuli, whereas those still in their native pools give evidence of it.

Further investigations have shown the correctness of Allabach's contention (1905) that in *Metridium marginatum* some individuals on mechanical stimulation reverse their ciliary stroke readily, others less readily, and still others not at all, variations largely dependent upon whether the animals have been starved or fed. Two underfed specimens of *Metridium* which on being tested were found to reverse their cilia to clean filter-paper were vigorously overfed and after three hours were tested again with bits of clean filter-paper. In both instances the paper failed to bring about a reversal of the cilia and consequently was rejected. In another test made eighteen hours after feeding, the paper was engulfed, showing that the cilia had returned to the state characteristic of animals that had lacked food. It is, therefore, clear that an underfed *Metridium* will reverse the effective stroke of its oral cilia to mechanical stimulation, though a small supply of food will obliterate this peculiarity and leave these organs incapable of such reversal.

The occasion of this loss of the power to reverse the stroke of the oral cilia on mechanical stimulation has been ascribed by Allabach (1905) to the difference in metabolism between a well-fed and an underfed indi-

vidual. This has been tested by cutting out the œsophageal tubes from several specimens of *Metridium*, laying them open and experimenting with them as ciliated membranes. If they are carefully prepared from animals that have not been recently fed, they will show a well-marked ciliary reversal to pieces of clean filter-paper. To fragments of mussel they reverse the ciliary stroke in the way characteristic for food, and after a dozen or more such trials they will no longer reverse to pieces of clean filter-paper. Thus the isolated membrane exhibits all the changes that it does as a part of the whole animal and under conditions where it is quite obvious that the one change that it has suffered is fatigue. It is, therefore, believed that the general metabolism of *Metridium* is not so much concerned with the change in the character of the response of the cilia to filter-paper as the fatiguing of the receptive mechanism of the ciliated surface is. In the undisturbed state this mechanism is at its greatest sensitiveness, but, on feeding, its efficiency diminishes and hence filter-paper no longer excites a reversal, a change which is now called forth only by the more vigorous stimulation from the dissolved products of the food. Hence the activities of the oral cilia are probably even more independent of the rest of the actinian than Allabach (1905) was inclined to insist upon.

The feeding movements of the tentacles in actinians are obvious neuromuscular reactions, as their disappearance on narcotization with chloretone amply shows. The independence of the individual tentacles in their feeding reactions has been demonstrated in a number of forms, in which these responses have been observed after the tentacles have been cut from the polyp. That one tentacle can influence another through connections in the

oral disc has been proved for *Condylactis* and is probably true for *Metridium*. The muscular responses of the tentacle in feeding, therefore, give much more opportunity for unified action than do the ciliary responses just considered.

That tentacular responses in actinians change with continued activity has long been recognized. Jennings (1905) found that the tentacles of *Stoichactis* after they had been vigorously plied for a while with meat ceased for a time to react to food. Allabach (1905) noted that in *Metridium* the tentacular reactions became gradually slower or even ceased as feeding progressed, and the same is recorded by Gee (1913) for *Cribrina*. Evidence of this in *Metridium* was long ago published (Parker, 1896) and recent work on this point has been entirely confirmatory.

Jennings (1905) attempted to explain this change as due to loss of hunger,[1] but Allabach (1905) showed that it also occurred when the tentacles were stimulated, though the animal was not allowed to swallow the food. Her conclusion is that it is simply the effect of fatigue. Gee (1913), however, declined to accept this explanation because if an actinian that will ordinarily show this tentacular change after having been fed eight or ten times, is experimented upon when in a fresh condition and is made to contract about the same number of times, its tentacles are found not to have lost their responsiveness. But both Allabach and Gee have failed to recognize that there are several kinds of fatigue. It is perfectly clear,

[1] It is perhaps unfortunate that the term hunger should have been used, for it is somewhat ambiguous. Usually it stands for a well known sensation due to movements of the stomach (Cannon and Washburn, 1912); less commonly for insufficient bodily nutrition. Pathology has long since demonstrated that these two phenomena are not necessarily connected, but in which sense Jennings intended to use the term is not always wholly clear.

from Gee's experiment, that muscular fatigue is not accountable for the change in the responsiveness of the tentacles, but it is entirely possible that it may have been caused by sensory fatigue. It is a common observation that if a sensory surface is placed under active stimulation, it is often only a short time before it will fall off very considerably in its receptiveness, and it is this form of fatigue in all probability that is accountable for the change in the tentacular responses of *Metridium* on continuous feeding. A repetition of Allabach's experiment of placing food on the tentacles of *Metridium* and, after they have responded, of removing it from the lips before it has been swallowed has in all instances confirmed her results; namely, the tentacles fall off in responsiveness. In view of what has already been stated it seems impossible to explain this phenomenon except as a result of sensory fatigue.

But there are also changes in the tentacular responses of actinians that are by no means so easily explained as are those that have just been considered. Jennings (1905) states that when the tentacles on the left side of an *Aiptasia* were plied with crab meat, they transferred the food to the mouth quickly five times, after which they reacted slowly on the sixth trial and hardly at all on the seventh. On trying the meat on the tentacles of the right side, it was found that the transfer to the mouth was quickly accomplished. Returning now to the left side, four sluggish deliveries were effected, after which the right side would now take no meat at all. Allabach (1905) states that *Metridium* can be fed from one side of its disc till no more food will be accepted, whereupon food will likewise not be accepted by the tentacles of the opposite side. Gee (1913) has also recorded essentially the same

condition in *Cribrina*. From these observations it seems clear that changes induced in the muscular responses of the tentacles of one side influence to no small degree the reactions of the tentacles on the other side. As Jennings (1905) has put it, the animal reacts as a unit, one side influencing the other. Experiments of this kind have been repeated on *Metridium*, and though the results were not so striking as those described by the authors already quoted, it was clear that when a *Metridium* was fed persistently by means of the tentacles of one side and so as to avoid touching with the food those of the other side, the opposite tentacles were nevertheless eventually influenced in their reactiveness and became less responsive as the feeding proceeded. Here would seem to be a good instance of some such general effect as that of changed metabolism or the general utilization even of nervous experience.

To ascertain whether changes in the tentacular responses of one side of the disc are transmitted nervously to the other side, small pieces of mussel were fed to the tentacles of one side of a *Metridium* but removed before they were swallowed and then, after the tentacles of that side began to lose in responsiveness, those of the other side were tested to see if they too had lost in their capacity to respond. The time in seconds required for the swallowing of each piece of food is recorded in the following table. The rejection of a piece of food is indicated by the sign of infinity.

It must be evident from an inspection of Table 3 that the right side of the animal gave no evidence of having been influenced by the left and that therefore there is no ground for the assumption that the experience of one side is transmitted nervously to the other. In other experi-

TABLE 3.

TIME IN SECONDS FOR THE TRANSFER BY THE TENTACLES OF METRIDIUM OF SMALL PIECES OF MUSSEL TO THE MOUTH WHEREUPON THEY WERE REMOVED AS THEY WERE ABOUT TO BE SWALLOWED. SIXTEEN TRIALS WERE MADE ON THE LEFT SIDE AND THEN THE SAME NUMBER ON THE RIGHT. ∞ INDICATES A DISCHARGE OF THE PIECE OF MEAT AT THE PERIPHERY OF THE ORAL DISC.

	Number of the Trial															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Left side of disc........	284	121	107	86	103	92	71	58	∞	97	108	∞	∞	72	∞	∞
Right side of disc........	72	86	306	63	112	∞	83	132	74	96	103	97	86	62	78	109

ments, in which the fragments of mussel delivered to the tentacles of the first side were allowed to be swallowed instead of being removed, the tentacles of the opposite side very regularly exhibited a decline in responsiveness. It is, therefore, believed that this change is due to the food introduced into the digestive cavity, and, since the pieces of food were very small, not to the accidental transfer of food juices from the side of the disc stimulated to the other, as suggested by Gee (1913).

To remove any doubt on this point a modification of an experiment tried by Gee (1913) was adopted and by means of a fine glass syringe a considerable amount of mussel juice was injected through the column wall of small specimens of *Metridium* into their digestive spaces. This operation was easily accomplished, especially if the region through which the puncture was made was previously anesthetized with magnesium sulphate. The injected juice apparently did not escape from the mouths of the animals, which, however, took in a considerable amount of seawater and enlarged, much as well-fed actinians do. After an hour or so the tentacles of the injected actinians were tested with fragments of mussel and

found to be very noticeably insensitive to food. It, therefore, seemed clear that it was the food in the digestive cavity rather than any accidental overflow that had influenced the tentacles.

Reasons have already been pointed out for believing that the change in the responses of the tentacles after continuous feeding is due to sensory fatigue and not to a general metabolic change; this seems also to be true in the particular instance under consideration. Though the meat juice injected into the digestive cavity unquestionably serves as material for metabolism and eventually must have its influence on the animal's general state, its first condition is that of a component of the fluid mixture that bathes the inner surfaces of the actinian. These surfaces include the cavities of the tentacles. As shown elsewhere (Parker, 1917 *b*), substances in solution in the digestive space of such organs as the large tentacles of *Condylactis* penetrate in a very short time the thin walls of these parts and thus make their way to the exterior. In doing so they must come in contact with the sensory ectoderm. Since the changes in the reactions of the tentacles produced by food juices injected into the digestive cavity are in the direction of diminished response, and since these changes come over the tentacles with considerable rapidity and before a modified metabolism dependent upon new food could have got much headway, it is believed that the loss of responsiveness in this instance, like that in the former case, is due to sensory fatigue and not to changed metabolism. In the first instance the fatigue was produced by the direct application of stimulating substances to the exterior of the tentacles; in the second to the transfusion of those substances from the cavities of the tentacles to their sensory mechanism. If

this explanation is correct, as there is good reason to suppose it is, the responses of the tentacles are like those of the oral cilia in that they are not especially dependent upon the condition of the animal as a whole. As Gee (1913) states, "the view that the seat of the modified responsiveness lies very largely in the individual tentacles is more clearly in accord with what is known of the structural organization of the sea-anemone than that the animal acts as a unit."

The feeding habits of sea-anemones thus prove on examination to consist of operations none of which necessitate the assumption of activities other than those consistent with the nature of the nerve-net. There is no reason whatever to resort to the hypothesis of a controlling nerve center. All the activities are strikingly local and the changes that they exhibit are apparently entirely due to fatigue. In these respects they are in strong contrast with the feeding habits in the higher animals, a process which has become so deeply wrought into the make-up of these forms that its relation to the animal as a whole is most profound. While almost every one of the elements involved in the feeding of actinians may be experimentally isolated and made to act for itself in a remarkably local way, scarcely any such independence is observable in the parts concerned in the similar operations of higher animals; the jaws and their muscles, buccal glands and so forth in these higher animals exhibit a highly unified action dependent chiefly upon central nervous connections such as is scarcely suggested in actinians, but as isolated elements they have almost no reactive power at all as compared with what is possible in sea-anemones. The feeding habits in actinians then emphasize the relative independence of parts rather than the action of the organism as a whole (Parker, 1917 *d*).

CHAPTER XII

OTHER COMPLEX RESPONSES AND THE NERVE-NET

As the locomotor activities of most actinians are extremely limited, the chief protective response of these animals is general retraction whereby they are reduced greatly in bulk, their more delicate parts are brought under cover, and they shrink close to the substratum to which they are attached. In many instances, in fact, retraction brings about a withdrawal of the body of the actinian into deep, rocky recesses and the like whereby very efficient protection is secured. The reverse process, expansion, is one which involves an enlargement and protrusion of the body as a whole and the opening of its folded surfaces and apertures in such a way that the operations of feeding, respiration, and so forth, may be resumed.

Retraction and expansion are relatively simple processes. Retraction in its initial phases is chiefly the result of the action of the mesenteric muscles, the longitudinal muscles of the non-directive mesenteries depressing the oral disc, those of the directives serving chiefly to fold the siphonoglyphs, and the parietal muscles acting on the column wall. After the depression of the oral disc has proceeded somewhat, the contraction of the sphincter muscle completes the process by bringing the oral disc under cover through the puckering effect of this muscle on the column wall. Incidentally the process of general retraction involves the expulsion of almost all the water contained in the digestive cavity of the actinian.

The reverse operation, expansion, is dependent first of all upon the relaxation of the sphincter and of the mesenteric muscles; then follows the slow filling of the digestive spaces with seawater through the ciliary currents in the siphonoglyphs; and probably as a last step the circular muscles of the column contract on the fluid contents of the body whereby the oral disc is forced well up above the pedal attachment. The details involved in the processes of retraction and expansion allow retraction to be accomplished much more quickly than expansion. This relation has all the appearance of an adaptation, for the quickness of a withdrawal may often be the essential part of the protection given by retraction, whereas there is nothing about the economy of an actinian, such as feeding, respiration, and so forth, that makes it vitally important for the animal to expand quickly.

The conditions under which a *Metridium* remains fully expanded are by no means simple, but include an aggregate of factors. In the laboratory the fullest expansion was obtained when the animals were in well-oxygenated, cool, running seawater in the dark. Under such circumstances this sea-anemone will extend itself to as much as six times the diameter of its column, and hold its oral disc fully opened. In nature a greater degree of expansion than that seen in the laboratory under the circumstances just stated apparently does not occur. This maximum degree of expansion under natural circumstances has often been observed in sea-anemones in pools during the night or even during the day in dark situations such as under bridges and so forth. The elements that contribute to this extreme expansion are certainly diverse. Of these light, temperature, food, oxygen supply, and water currents are of significance.

The influence of light on actinians is by no means uniform but differs with different species. According to Nagel (1894, 1896), *Adamsia, Anemonia,*[1] and *Actinia* are not responsive to light. Fleure and Walton (1907) have noted this lack of response in *Anthea* as well as in *Adamsia.* Piéron (1906 *c*, 1908 *c*) has confirmed Nagel's statment for *Actinia.* Although this lack of response may be true of the forms just mentioned, it is certainly not true of *Metridium marginatum* or *Sagartia luciæ,* for, though Hargitt (1907) was unable to get responses to light from these species, both will close quickly on bright illumination. This is in agreement with Bohn's observations (1906 *a*) as well as with Gosse's account (1860) of the closely allied species, *Metridium dianthus.* Concerning this form Gosse remarks that "it is under the veil of night that the anemones in general expand most readily and fully. While the glare of day is upon them, they are often chary of displaying their blossomed beauties; but an hour of darkness will often suffice to overcome the reluctance of the coyest. The species before us [*M. dianthus*] is not particularly shy; it may often be seen opened to the full in broad daylight; but if you would make sure of seeing it in all the gorgeousness of its magnificent bloom, visit your tank with a candle an hour or two after nightfall." Retraction under bright illumination has also been recorded for a number of actinians among which are the following: *Edwardsia*[2] (de Quatrefages, 1842; Fischer, 1888), *Cerianthus*[2] (Haime, 1854; Nagel, 1894; Hess, 1913), *Phillia* (Gosse, 1860), various species of

[1] Bohn (1907 *c*) states that *Anemonia* is not entirely without response to light. In weak light it is said to place its tentacles at right angles to the rays and in strong light parallel to them.

[2] These instances, *Edwardsia* and *Cerianthus*, are often attributed to Bronn (1860) who apparently simply repeated the statements made by de Quatrefages and by Haime without giving references.

Sagartia (Gosse, 1860; Fleure and Walton, 1907; Hargitt, 1907; Piéron, 1908 *c*), *Paractis* (Jourdan, 1879), *Cladactis* (Hertwig, 1879-1880), *Aiptasia* (Jennings, 1905), *Tealia* (Fleure and Walton, 1907), *Eloactis* (Hargitt, 1907), *Ceractis* (Schmid, 1911), and *Bunodes* (Hess, 1913). Although closure in the presence of light is the ordinary form of response for most actinians there seems to be good evidence that a few react in the opposite way. *Actinia equina,* according to Bohn (1908 *a*), is expanded in the daytime and retracted at night, and the same is true of *Cribrina zanthogrammica* as observed by Gee (1913), who also adds that a closed *Cribrina* in the dark will expand under the influence of a 32-candlepower light. Both *Actinia* and *Cribrina* contain symbiotic algæ in their tissues, and it is easy to imagine that their expansion in daylight may be an advantage so far as photosynthesis is concerned, but whether this expansion is a reversal of the usual form of actinian response to light or is due to the effects of some such substance as oxygen which may be given off by the symbiotic algæ in the light is not known. It thus appears that aside from a few indifferent actinians and a few that open in the light, the majority respond to the stimulus by retraction. In this respect, as already intimated, *Metridium* is not exceptional.

If a fully expanded *Metridium* in the dark is suddenly exposed to diffuse daylight, it will shorten its column to one-third or one-fourth its former length and with its oral disc fully expanded remain in this state more or less continuously. The shortened state produced in *Metridium* by general illumination represents the ordinary condition in which many of these sea-anemones are found in nature during the daytime. If on such a partly contracted *Metridium* a beam of reflected sunlight is thrown,

the animal will after a minute or so almost invariably shorten its column completely and contract its oral disc, thus assuming the condition of complete retraction. This state is commonly met with in nature as a result of direct exposure to sunlight. It occurs in situations where the sea-anemones are subjected during a part of the day to shadow and during the rest to full sunlight. Under the latter circumstances they are almost invariably fully retracted; under the former they are more or less expanded.

When a fully expanded *Metridium* in running water in the dark is illuminated either from the side or from above by a 16-candlepower electric light at a distance of half a meter the animal will shorten considerably but, as a rule, will not cover its oral disc. This is occasionally induced by very strong artificial illumination, but it is a reaction by no means easily called forth. It is, however, often enough met with to warrant the conclusion that so far as light is concerned *Metridium* will undergo complete contraction of both column and oral disc only in the very brightest illumination; that in weaker light it shortens the column but does not cover the oral disc and that its fullest expansion is called forth only in complete darkness.

The effect of temperature on actinian response has been little studied. Specimens of *Metridium* upon which observations were made were kept in an aquarium with running seawater, the temperature of which was about 23 degrees centigrade. The temperature of the outside water from which the supply for the aquarium was obtained was about 21 degrees centigrade (August). At such temperatures, as was to be expected, the animals remained expanded when the other conditions were appropriate, and normally responsive. When the animals were

supplied with running seawater that had been artificially cooled to about 8 degrees centigrade, they remained fully expanded in the dark and would shorten in the light. They responded to a mechanical stimulus by contraction, and in other respects they reacted as they did under more usual temperatures.

If sea-anemones in seawater at 23 degrees centigrade are flooded with water at 35 degrees centigrade, even though they are kept in the dark, they invariably contract completely. This response is in general agreement with what was found by Fleure and Walton (1907), namely that *Actinia* and *Anthea* retract at temperatures above 22 degrees centigrade. If, however, *Metridium* is subjected to a gradual change of temperature which eventually reaches 36 degrees centigrade, it slowly loses its responsiveness to mechanical and chemical stimuli and soon dies. The loss of responsiveness begins at about 34 degrees centigrade, and is complete at 36 degrees centigrade. An animal kept a few minutes in seawater at 35 degrees centigrade may be touched repeatedly on the column near the pedal disc without showing any response and may be eventually killed in alcohol in an expanded condition. Animals which have thus been rendered insensitive seldom recover, but in the course of a day or so die.

So far as *Metridium* is concerned, subnormal temperatures have little influence on its responsiveness except possibly on the rate. Supernormal temperatures, if quickly applied, induce general contraction; if gradually applied and of sufficient intensity (35 degrees centigrade), they bring about a condition of non-responsiveness that quickly passes over without contraction into one of death. Whether the tentacles are receptors for temperature

changes, as maintained by Nagel (1894), cannot be stated at present.

Many observers in the past have noted that retracted sea-anemones can be induced to expand by placing pieces of meat or other food so near them in the water that dissolved materials from this food are wafted to the animals. Pollock (1883) and Romanes, in consequence of such observations, were led to assume the presence of the olfactory sense in these animals. More recently this response to food has been observed in *Metridium* by Allabach (1905) and in *Actinia* by Piéron (1906 *b*, 1906 *c*). Allabach's statements can be confirmed easily on *Metridium*. If into two large glass dishes of fresh seawater many specimens of contracted *Metridium* are placed and into one of these dishes is poured a small amount of juice from a crushed mussel, the sea-anemones in that dish almost without exception will expand their oral discs in a very few minutes, whereas those in the other dish will remain almost to an individual retracted. It was quite clear from observations of this kind that the dissolved products from the food of the sea-anemone would induce the expansion of its oral disc, though this agent had very little effect on the shortened condition of the column in these animals.

The part played by oxygen in the expansion and retraction of sea-anemones has been a matter of recent dispute. According to Piéron (1906 *b*), *Actinia equina* opens in seawater with a large oxygen content and closes when there is a deficiency of this gas. Piéron (1908 *a*, 1908 *b*, 1909), as a result of further investigations, was led to believe that not only did oxygen have this effect but that it was one of the most important factors in determining expansion and retraction. Bohn (1908 *a*, 1908 *c*, 1910 *a*),

on the other hand, maintains that *Actinia equina* will remain expanded in seawater containing very little oxygen and will close when that water is richly oxygenated. In the opinion of this investigator the states of expansion and retraction are due chiefly to light and darkness and not to the supply of oxygen. In the face of such differences of opinion it is difficult to arrive at any conclusion without further observation.

Specimens of *Metridium marginatum* in the rock pools at Woods Hole, Massachusetts, were therefore studied. The pools in which these sea-anemones were located were flooded at high tide and left isolated at low tide. The oxygen content of the seawater from the several situations involved was determined by the Winckler method.[3] The outside water on the incoming tide was found to contain 7.06 milligrams of oxygen per 1000 cubic centimeters. The water in a small undisturbed pool just previous to the entrance of the tide contained 3.15 milligrams of oxygen per 1000 cubic centimeters, while that in the undisturbed end of a pool into which the tide was beginning to flow, contained 2.76 milligrams. At the end of the pool into which the tide had entered, the oxygen was found to be 7.02 milligrams per 1000 cubic centimeters. From these figures it is evident that at the time of observation the water in the pools contained decidedly less than half as much oxygen as that in the flowing tide and that the entrance of the tide into a pool quickly changed the water there from a condition poor in oxygen to one relatively rich in this gas. Another point of difference in the water of the pool and that of the flowing tide was that the pool water had a temperature of about

[3] The determinations were made by Dr. H. Wasteneys.

27.5 degrees centigrade and that in the inflowing tide 21.5 degrees centigrade.

Experiments to ascertain the effect of the oxygen in the several kinds of water on *Metridium* were conducted under the following conditions. The pools, which were on Pine Island, in Woods Hole, Massachusetts, were studied on clear days in August. Work was begun as the tide was rising, but before it had reached the pools. In bright daylight almost all the specimens of *Metridium* were retracted. Large battery jars were carefully filled with water from the pools and into these jars stones were put, having attached to them several specimens of *Metridium* in the retracted condition. The jars were allowed to stand in the same exposure as the pool to determine whether the act of transferring the sea-anemones would influence their conditions. As a matter of fact, the animals remained closed and gave no evidence of being in any other state than that of the actinians that remained in the pools. Careful transfer from pool to jar is, therefore, not a source of disturbance to *Metridium*.

If, now, pieces of stone on which there are closed actinians are quickly transferred from the pools to the outside tidal water, many of the sea-anemones on them will in a few minutes expand their oral discs though their columns will remain contracted. This response, though not invariable, was of such common occurrence that it was quite obviously typical of the transfer. It must depend upon some difference between the two bodies of water, for as has already been shown, the act of transfer in itself is without significance. The difference between the two bodies of water are differences of temperature, oxygen content, and current action.

To ascertain the effect of temperature, carefully col-

lected pool-water was cooled by being surrounded with ice from its initial temperature of 27.5 degrees centigrade to that of the outside tidal water, 21.5 degrees centigrade. Into this cool pool-water pieces of rock on which were closed actinians were introduced from the pools, and the animals watched. They remained contracted for over an hour and it was concluded that the expansion of the sea-anemones when transferred from the pools to the outside tidal water was not due to the difference in temperature.

Pool-water was now collected and thoroughly aërated by being poured back and forth from one jar to another many times, but when placed in this the sea-anemones also failed to expand. Some of this water on being examined proved to contain 7.33 milligrams of oxygen per 1000 cubic centimeters. It is, therefore, clear that *Metridium* does not expand in the running tide because of the increase of oxygen.

Finally two jars were so arranged that one conducted water into the other through a large siphon in such a way as to expose the flowing water to air as little as possible. The upper jar being kept full of pool-water, supplied the lower jar from which the water was in continuous overflow. In this way pool-water was given a current without changing in any marked degree its temperature or its oxygen content. When closed specimens of *Metridium* on bits of rock were introduced into the jar through which the water was flowing, they very commonly expanded their oral discs though their columns remained short. It, therefore, seems clear that the motion of the tide water, rather than its lower temperature or greater oxygen content, was the element responsible for the expansion of *Metridium* under the circumstances noted. As a check

on this conclusion several vessels were filled with tidal water and after it had come to rest stones carrying *Metridium* were introduced into it. Although this quiet tidal water retained its characteristically lower temperature and its higher oxygen content, the sea-anemones remained closed in it, thus confirming the conclusion already expressed that motion is the element in tidal water that induces expansion.

The effect of water currents and other forms of agitation were not only observed under natural conditions but were tested likewise in the laboratory. If a *Metridium* is put in a darkened vessel through which seawater is running, it quickly assumes a condition of maximum expansion both as to its oral disc and its column. If, now, the current is shut off, in about a quarter of an hour the oral disc will be found covered, but the column will remain more or less elongated. The same was found true of groups of *Metridium* on stones. Five, in one group, were made to expand fully in running seawater in the dark. The current was then cut off and in eighteen minutes the oral discs of all five specimens were covered and some of the animals a little shortened. An hour and a half after the current had been stopped all were still closed except one which had partly expanded its oral disc. Still an hour later all were retracted, whereupon the current was reëstablished and in seven minutes all were expanding, a process completed by all five in about thirteen minutes. These responses were found to occur as well at 8 degrees centigrade as at the more usual temperature of 21 degrees centigrade.

The agitation of the seawater, in a purely mechanical way and without reference to oxygen and the like, appears, therefore, to be a means of inducing the expansion

of *Metridium*, especially of its oral disc. This form of reaction has already been observed in *Actinia* by Piéron (1906 *b*, 1908 *d*), who, however, points out that certain forms of mechanical agitation also induce retraction (Bohn, 1907 *a*).

Since the expansion of the oral disc is dependent chiefly upon the relaxation of the sphincter muscle, it seems probable, as already pointed out (Parker, 1916 *a*), that the mechanical stimulus of the moving water in one way or another has a very specific effect on this muscle. The condition of relaxation thus induced is apparently exactly like that seen in such sponges as *Stylotella*, where the oscular sphincter remains relaxed in running water but contracts when the current ceases (Parker, 1910 *a*).

The foregoing account shows quite clearly that the expansion and retraction of such a sea-anemone as *Metridium* is dependent upon a variety of factors. Light and high temperature, especially when suddenly applied, produce retraction; food and water currents, expansion; the oxygen supply, in *Metridium* at least, seems to have very little, if any, direct influence on retraction and expansion.

These operations in sea-anemones have been regarded by some investigators, notably Bohn and Piéron, as occurring in rhythmic fashion, and two types of rhythm have been distinguished; a tidal rhythm and a daily or nychthemeral rhythm. According to Bohn (1906 *b*, 1909, 1910 *b*) *Actinia equina* retracts when it is exposed to air by the falling tide and expands when it is again covered by water, and this rhythm may be retained for from 3 to 8 days in an aquarium though the animals under such conditions are always under water. Piéron (1908 *c*), on the contrary, questions the presence of a pronounced tidal rhythm in *Actinia equina*.

Metridium marginatum is found commonly either below low-water or in pools that do not empty on the falling of the tide. When exposed to the air it usually retracts, though this is not invariable. This species, partly from the situations in which it is found and partly from its irregularity of response, is not a very favorable one in which to seek evidence of tidal rhythm.

In this respect *Sagartia luciæ* is very much more promising. This species attaches itself to stones, shells, and other fixed objects that are commonly exposed to air by the falling tide. When thus exposed this species is very regularly retracted, and when covered with water it is expanded though not invariably so. To ascertain whether this rhythm would persist, as maintained by Bohn for *Actinia,* stones covered with *Sagartia luciæ* were transferred to an aquarium and record was kept of the subsequent condition of these actinians. The results were quite uniform and may be well illustrated by a single example.

On July 7 at 11.00 in the morning a stone that had been exposed by the tide for some hours and that had upon it twelve contracted *Sagartia* was transferred to an aquarium. At half past eleven all the sea-anemones had expanded and they remained so for the next thirty hours, after which they began to close irregularly. Similar conditions were repeatedly observed and it, therefore, seems quite certain that in *Sagartia luciæ* there is no persistence of a tidal rhythm. In this respect these observations agree with those of Gee (1913) on *Cribrina,* where no trace of the persistence of tidal rhythm could be discovered.

Metridium marginatum is almost always under water and is so responsive to light that it might well be sus-

pected to be a species that would exhibit a pronounced daily or nychthemeral rhythm. On August 9th, at 10.30 in the morning, a large pool in full sunlight was plotted and twenty large specimens of *Metridium* were accurately located. All were fully retracted. At 10 o'clock on the evening of the same day, the sky being overcast with clouds and the night dark, the pool was again visited and by means of a hand light the twenty sea-anemones were reidentified. All were fully expanded. A number of other observations of this kind and many casual records were made of the condition of pool animals in daytime and at night, and always with the same results; completely retracted in the day. Observations on sea-anemones in dimly lighted situations, such as under bridges and so forth, showed that these animals were more or less continuously expanded, but aside from such exceptions it was clear that *Metridium* in its natural surroundings exhibited a well-marked nychthemeral rhythm.

This form of rhythm agrees with what Hargitt (1907) has observed in *Eloactis*, and Piéron (1908 *c*) in *Sagartia troglodytes*, and what has been claimed by Bohn (1906 *b*, 1907 *b*) to occur in *Actinia equina*, though the nychthemeral rhythm in this species has been questioned by Piéron (1908 *c*, 1908 *e*). That in *Metridium* it is dependent upon light, as maintained in general by Bohn (1908 *a*, 1910 *a*), and not upon oxygen, as was claimed for other species by Piéron (1908 *c*, 1908 *e*), has already been shown.

Nothing apparently has ever been observed about the activities of *Metridium* that would lead to the supposition that its nychthemeral rhythm is ever reversed or is ever exchanged for a tidal rhythm as has been claimed for some species by Bohn (1908 *b*, 1909).

A persistence of the nychthemeral rhythm in *Metridium* after its removal from the influence of day and night is apparently as little in evidence as the tidal rhythm in *Sagartia luciæ*. Specimens of *Metridium* in a retracted condition were removed from a quiet pool at noon and placed in running water in the dark. In less than an hour all were fully expanded and remained so for over 36 hours. These observations agree with those of Gee (1913), who was unable to find any evidence for the persistence of the nychthemeral rhythm in *Cribrina*.

That sea-anemones may exhibit in the sequence of their states of expansion and retraction a tidal rhythm or a nychthemeral rhythm, as pointed out by Bohn and by Piéron, there can be not the least question, but that these rhythms may persist even for a few days in the absence of the external stimulus, as maintained especially by Bohn, is certainly not true for *Metridium marginatum* or *Sagartia luciæ*. The fact that a persistence of rhythm in aquarium specimens has not been seen by Appellöff (Retterer, 1907), Gee (1913), and others throws grave doubt on the occurrence of this phenomenon at all, but a decisive answer to this question can not be given till the species for which these peculiarities have been claimed is reinvestigated.

Bohn and Piéron (1906) and especially Piéron (1906 *b*, 1908 *a*, 1910) have claimed that in *Actinia equina* the tidal rhythm is carried out a little in advance of the actual tidal changes, thus giving evidence of what may be called an anticipatory reaction. This reaction, according to Piéron (1910), may be lost when the animals are placed in an aquarium and may be regained after a week or so when they are again subjected to the tides. *Metridium* has been watched very

closely for signs of this preparatory activity, but no conclusive evidence of it has ever been observed. It is astounding how quickly *Metridium* will begin to expand on the entrance of the tide into a pool in which this sea-anemone is located. With this species expansion often begins within a few minutes after the arrival of the first new tidal water. As already pointed out, this expansion appears to depend upon the movement of the water and not upon its temperature or its oxygen content. Since the first water that enters the pool, often by indirect and not easily visible channels, may cause all the water in the pool to move somewhat, a stimulus imperceptible to the observer may be given to every actinian there and thus induce expansion in what seems to be an anticipatory manner, whereas in reality it is a response to a direct stimulus. It is in some such way as this that Piéron has probably been deceived, for Bohn (1908 *a*) is very likely correct in questioning the existence of reactions really anticipatory. Such rhythms as have thus far been studied in sea-anemones seem, therefore, to depend upon immediate rhythmic stimuli external in origin, as the changes of the tides or the change from day to night and the reverse, and not upon rhythmic organic operations of a more internal nature.

In jellyfishes rhythmic movements are seen in the pulsing of the bell. In this instance, as already pointed out, the normal pulse depends very commonly on certain sense organs. These are often grouped together and constitute the so-called marginal bodies. There are commonly eight or more of these bodies on each bell. Their complete removal, as already mentioned, is followed by at least a temporary cessation of pulses. It is also well known that the presence of a single marginal body is all

that is necessary to keep up continuous pulsing. How, under normal conditions, the eight or more centers in a pulsing bell are coördinated has been a question of much interest. Romanes (1878) has shown that if a scyphomedusa is partially subdivided by radial cuts that run from the edge of the bell well toward its center and alternate with the marginal bodies so that each segment thus

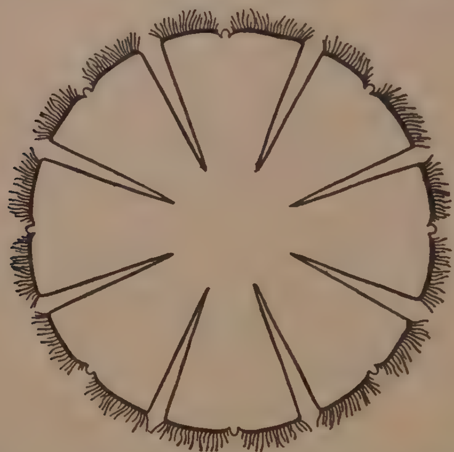


FIG. 42.—Diagram of a jellyfish *Aurelia* whose bell has been deeply incised in a radial direction at eight places reducing it thus to partial octants each one of which carries a marginal body. As shown by the experiment of Romanes, each octant has its own rate of pulsing.

formed carries a single one of these bodies (Fig. 42), the segments thus formed continue to pulse but not in unison, for each will have its own rate. Loeb (1899) has shown that the apparent coördination of the group of marginal bodies or like organs in the medusæ is due not to a coördinating center but to a condition such as is seen in the radially cut bell, except that in the normal bell the response from the marginal body that for the moment has the most rapid rate stimulates all the others to action and thus one body temporarily controls the whole bell.

With the exhaustion of the given marginal body, the control naturally passes to the most active of the remaining bodies. Thus the rate of pulsing would be determined first by one, then by another marginal body, depending upon the temporary physiological state of these parts. Hence this type of rhythmic activity presents no element that calls for centralized control, a condition that would be difficult to harmonize with what is known of the nerve-net. It is the result rather of the state of the marginal bodies which, as von Uexküll (1901) has shown, can be thrown into action by so slight a movement as that produced by the elastic recovery of the bell after its pulse.

Another form of response that may be taken as indicative of the nature of the nerve-net in actinians is locomotion. Gosse (1860), a most enthusiastic and industrious student of these animals, after watching the creeping of *Sagartia pallida,* wrote that "it was impossible to witness the methodical regularity of the process, and the fitness of the mode for attaining the end, without being assured of the existence of both consciousness and will in this low animal form." Such an opinion, however, was rather the result of an admiring devotion to an interesting group of animals than to a close scrutiny of their real performances, especially under experimental conditions. Pedal locomotion has already been discussed in an earlier chapter of this book where it was pointed out that this operation could be successfully performed by specimens of *Sagartia* from which the oral half had been cut away. Such fragments not only creep but creep away from the light as normal individuals do. In fact, their activities are not essentially different from those of whole animals. Creeping, then, is in no sense dependent upon the animal as a unit, but is an activity of the

pedal disc and adjacent parts. It is, however, an activity of the disc as a whole. Locomotion has never been observed in pieces of the pedal disc. When actinians are cut in such a way that the fragments retain only parts of the original pedal disc, they remain attached to the substratum by their pedal surface, but they never exhibit locomotion. It is only after regeneration has set in and a new pedal disc has been established that locomotion recommences. Creeping then is a response which calls for a much more unified mechanism than feeding, and Lukas (1905) is probably correct in regarding it as a response that gives evidence of the highest form of nervous activity thus far discovered in actinians. That it is indicative of a primitive form of desire and hence discloses the beginnings of consciousness as asserted by Lukas (1905) can be neither proved nor disproved. But of its importance as showing a certain amount of unity in actinians there can be not the least doubt.

Another line of investigation that is suggestive of more than the simplest form of nervous activity in actinians is the modifiability of their responses. This subject has been investigated by Jennings (1905), who has shown its significance by direct experiment. If a drop of water is allowed to fall on the surface of the water in which an expanded *Aiptasia* rests, the animal will usually retract. After expansion a second drop often fails to call forth any such response and in fact it is necessary to allow, as a rule, an interval of five minutes before a second response can be elicited. Thus the earlier stimulus influences the neuromuscular apparatus of the sea-anemone in such a way that a repetition of the stimulus is not followed by a response. To put the matter as Jennings does, the previous history of an organism has its

influence upon its subsequent responses. This feature in actinian reactions is a special application of a principle that has long been familiar to physiologists. When an explanation of it is sought, one naturally turns, as in the case of the dying away of feeding responses, to exhaustion. Does not the initial stimulus, the vibration from the first drop of water, so exhaust the neuromuscular mechanism that it is incapable of receiving in an effective way a second stimulus till after a certain time for recovery?

This subject has been quantitatively studied by Kinoshita (1911), who has shown by the use of several kinds of weak stimuli that the responses to these fall off so rapidly that it is highly improbable that exhaustion plays any important part in the whole operation. Much more likely is it that the neuromuscular apparatus through its first response is brought into a state that is to be described as one of inhibition rather than of exhaustion. From this standpoint the condition left by the first stimulus and response is not unlike that seen in the refractory period of nerve and muscle. At least it is clear that the first response of the actinian has a relatively profound influence on the subsequent reactions of this animal and that this influence lasts long enough—five or ten minutes—to affect the outcome of later stimulation. Here, then, in the truly nervous activities of actinians is evidence of the beginning at least of nervous states analogous to the more complex conditions found in higher forms.

In attempting to make clear the conditions under which the second or modified response takes place, care must be exercised that confusion does not arise as to the nature of the explanation. To one class of workers, those

of a physiological turn, an explanation of the modified form of response is found in an understanding of the interaction of the second stimulus and the receptor, together with the chain of events that terminate in the muscular movement. This form of explanation is concerned exclusively with the working mechanism as such and has nothing to do with its historical origin. The second form of explanation, the one more likely to be adopted by those of a more biological bent, seeks for an understanding of the modified response in the influences that have emanated from the original response and thus bring that response into historical relation with the second and modified one. This form of explanation emphasizes the effect of the history of the animal on its immediate state. Both forms of explanation depend, of course, upon material changes that occur within the actinian, but in the first attention is directed especially to those changes that take place in the course of the modified response, whereas in the second emphasis is put on the changes that link the first response with the second.

The opinion that the past history of an individual actinian is a potent factor in understanding its behavior has been expressed not only by Jennings (1905) but also by Piéron (1906 *c*), who declared that in this respect the responses of actinians included traces of those activities characteristic of the central nervous organs of higher animals. But very little work has been done on actinians to ascertain the extent to which such central activities as those just indicated may extend. The limited range of response in these animals restricts such experimentation considerably. Heretofore associative processes have never been directly identified in actinians and repeated efforts in this direction have always yielded negative re-

sults. One set of experiments directed toward testing this question may be described.

Sagartia luciæ occurs commonly between high and low water marks and when exposed to the air it is retracted. If exposed for a long time, a day or more, it will dry up and eventually die from desiccation. Specimens of this species that had been creeping actively on a sheet of glass under water were exposed to air, whereupon they retracted and dried slightly on their outer surfaces. When this resting state had been assumed, the glass was set in an inclined position in a vessel of seawater and at such a level that the lower pedal edge of one of these actinians was just in contact with the water, the rest of the animal being exposed to the air. Although it would have been easy for this particular actinian to have crept down into the water, it remained inactive and fixed to the spot for over three days while its mates on the part of the glass that was under water crept about freely. Similar trials on other individuals always gave the same results; the actinians remained fixed. Had they crept into the water, it would have required further experimentation to have ascertained the reason for this, but, as they regularly did not, the observations give no grounds for the assumption of nervous activities of an exceptional order.

In examining the literature on the behavior of actinians two tendencies are quite obvious. One emphasizes the diffuse, non-centralized nature of actinian responses and deals with the behavior of these animals in terms of relatively simple reflexes and the like; the other brings into prominence the unified action of these animals and interprets their behavior from the standpoint of the whole organism. It is by no means clear that these dif-

ferences of opinion are really as pronounced as they sometimes appear on paper, but it is perfectly evident that the two general views represent real differences on a subject about which the truth can not at present be easily stated.

More or less of this difference is doubtless due to the various methods of attack which different investigators have used in this field of work. Since the external stimuli are more easily measured and otherwise controlled than the internal states, these were naturally first studied, with the result that the work of Loeb, Nagel, and others led to a general conception of an actinian as a delicately adjusted mechanism whose activities were made up of a combination of simple responses to immediate stimulation. This view has been criticized by Jennings (1905) as giving an unnaturally sharp, clear-cut and simple picture of actinian behavior. Jennings, moreover, has drawn attention to the physiological state of the animal, including the effects of previous stimulation, of its metabolism and so forth, in fact of its general past history, as an internal element of no small importance in interpreting its reactions. But this view is not without its serious limitations. As von Uexküll (1909) and Baglioni (1913) have recently pointed out, it too often tempts the worker to be satisfied with the statement of inferred internal states as explanations of conditions which upon careful scrutinizing prove to be dependent upon quite different factors, and the consequent vagueness and uncertainty with which it often surrounds the subject obscures the real questions for investigation.

Keeping in mind these two tendencies, what can be said about the psychology of actinians? First of all, it seems fairly certain that their behavior is chiefly deter-

mined by their immediate environment. They are expanded or retracted, feeding or quiescent, creeping or still in consequence of immediate stimulation rather than as a result of internal states due to past activities. They exhibit rhythmic responses only to immediate rhythmic stimuli, not to the effects of past rhythmic stimulation. As a result of their various activities their physiological states are changed and these changes unquestionably modify their capacity for renewed response, but such changes have not been found to be very lasting. From the evidence thus far accumulated, it appears that these states persist for only a brief period, often only a few minutes or at most some hours. It also appears that an actinian is much more nearly an organism whose internal state is one of general uniformity than one of great flux. On this uniformity as a background the changing environment calls forth now this, now that set of responses without, however, seriously disturbing the internal equilibrium. This condition of affairs is in strong contrast with what is found in the higher animals, where the responses to the environmental influences are extremely diverse and variable in consequence of the delicacy of internal equilibrium, and as a result these animals when subjected to experimental study often exhibit such novel and apparently unrelated responses that we are prone to speak of many of them as accidental or spontaneous. Spontaneity in this sense is not a characteristic of actinian behavior, which recalls very much more the relatively simple direct type of reaction as seen in such organs as the vertebrate intestine. It is with this type of reactive mechanism rather than with the cerebral cortex that the actinian shows affinity.

If such a view of the behavior of sea-anemones is cor-

rect, there is no reason to suppose that the unity of their organization is necessarily of a high order, as in fact the preceding accounts show. It seems quite certain that von Uexküll's description (1909) of one of these animals as a bundle of reflexes is inadequate, but it is also equally certain that this description is nearer the truth and certainly far freer from error than the picture drawn by Gosse (1860) of these forms endowed with consciousness and will. The facts that the pedal half of an actinian may creep normally without the oral half and that the oral half is responsible for the feeding activities through a concourse of semi-independent parts, tentacles, œsophagus, and so forth, make it quite obvious that the organic unity of the animal as a whole is very weak. As Piéron (1906 *a*) remarked, most parts of an actinian possess unusual autonomy. Or, to state the matter for the whole animal as von Uexküll (1909) has phrased it for the nervous system, the sea-anemone partakes more of the nature of a sum of parts than of a unit. The harmony of action that is encountered on most sides in actinian behavior is in reality indicative of very little of that kind of unity that pervades the individual higher animal. To speak of sea-anemones as having a psychology is to use this term in its very broadest sense (Piéron, 1906 *a*).

CHAPTER XIII

HYDROIDS

The study of the neuromuscular organization of the cœlenterates has been accomplished chiefly on representatives of the scyphozoa and anthozoa. In both these classes the individual animals are of relatively large size and for this reason scyphozoans and anthozoans have been favorable material for anatomical study as well as for experimental work. In the hydrozoa, on the other hand, the polyps and medusæ are generally quite small, even microscopic; consequently members of this class are much less favorable for investigation. The hydrozoa are, however, generally regarded as more primitive than the other two classes, and hence in a study of the elementary nervous system they deserve attention. This is particularly true in consequence of the outcome of some of the more recent work on the higher cœlenterates. These animals are provided with a neuromuscular mechanism that is by no means so simple as was supposed by many of the earlier workers. It not only includes independent muscles, but muscles associated with nerve-nets and muscles subject to reflex control. As hydrozoans are supposed to be simpler in their organization than the other cœlenterates, it is possible that their neuromuscular organization may partake of this simplicity and thus give some clue as to the evolutionary steps that have led from such conditions as those seen in the sponges to such as characterize the higher cœlenterates.

In carrying out such studies a reasonably large polyp

is desirable. Such a form is to be found in *Corymorpha palma* from the coast of southern California.

Corymorpha palma is a beautifully transparent, solitary hydroid of slender proportions (Fig. 43). Its stalk measures as much as 10 centimeters or more in length with a diameter at the thickest part of about 0.5 of a centimeter. Its proximal end is anchored in the mud and its distal end carries a hydranth that when expanded may have a spread of 2.5 centimeters. The proximal portion of the stalk ends in a blunt point and carries rows of long filamentous bodies, the frustules, by which it is anchored in the mud. This portion of the stalk, often half a centimeter or so in length, is commonly turned nearly at right angles to the rest, which is held vertically above the mud. A little

Fig. 43.—Side view of the hydroid *Corymorpha*, somewhat enlarged.

above the level at which the stalk emerges from the mud it gains its maximum diameter; distal to this it becomes gradually more and more slender till it reaches a narrow neck, on which the hydranth is borne. The stalk itself is marked by a series of longitudinal canals imbedded in its more peripheral substance and running for the most part

parallel to each other except toward the proximal end, where irregular cross connections are common. The proximal third of the stalk is covered with a thin perisarc, the rest being naked.

A fairly well marked constriction separates the stalk from the hydranth. The hydranth consists of a thickened disc attached to the distal end of the stalk and carrying on its periphery some twenty to thirty long tentacles, the proximal tentacles. From the middle of the outer face of the disc rises the proboscis, at the distal end of which is the mouth surrounded by about forty to sixty short tentacles. Immediately beyond the bases of the proximal tentacles, and taking their origin from the proximal part of the proboscis itself, arises a number of short peduncles, to which are attached fixed medusæ bearing the gonads. The appearance of *Corymorpha* as a whole is that of a delicate miniature palm tree whose substance seems to be translucent glass rather than animal matter.

The common reaction systems possessed by the majority of cœlenterates are the mucous glands, the cilia, the nettle cells, and the muscles. In *Corymorpha* the mucous glands are insignificant and it is very doubtful whether there are any cilia at all. Nettle cells are present and are apparently quite independent of nervous control.

The muscles of *Corymorpha* are few and simple in comparison with those of an actinian and have already been briefly described by Torrey (1904 *b*). The longitudinal muscle of the stalk (Allman, 1871–1872) is a sheet of tissue whose fibers run lengthwise that structure and are closely applied to the ectodermic face of the supporting lamella.

The circular muscle of the stalk (Allman, 1863) con-

sists of a sheet of fibers applied to the entodermic face of the supporting lamella and extending at right angles to those of the longitudinal muscle. Near the distal end of the stalk there is usually a marked constriction, which is apparently brought about by the excessive contraction of the circular muscle fibers of that region. This constriction suggests the presence of a specialized muscular sphincter, such as has been claimed by Riddle (1911) in *Tubularia,* but, as a special accumulation of fibers in this region appears not to be present, it seems scarcely appropriate to describe a sphincter muscle as distinct from the rest of the circular muscle of the stalk.

An ectodermic longitudinal muscle and an entodermic circular one occur in the proboscis exactly as they do in the stalk. In sections of both the proximal and distal tentacles longitudinal ectodermic muscles can be seen. The circular entodermic muscles mentioned by Torrey (1904 *b*) as present in the two sets of tentacles, have not been identified. If they are present, they must be relatively poorly developed, for, in material in which the longitudinal fibers could be clearly demonstrated, the circular fibers could not be seen, though the plane of section was entirely favorable for this purpose. *Corymorpha,* therefore, possesses at most only six muscles or groups of muscles: (1) the longitudinal muscle of the stalk, (2) the circular muscle of the stalk, (3) the longitudinal muscle of the proboscis, (4) the circular muscle of the proboscis, (5) the longitudinal muscles of the proximal tentacles, and (6) the longitudinal muscles of the distal tentacles. This enumeration does not include the longitudinal muscles of the peduncles of the sessile medusæ nor those of the medusæ themselves, whose activity, as Torrey (1907) has pointed out, implies the presence of

at least a subumbrellar band. In general the polyp of *Corymorpha* exhibits the arrangement of muscles found in the typical hydrozoan, a longitudinal ectodermic system and a circular entodermic one. The longitudinal entodermic system claimed by Lipin (1909) for *Polypodium* is associated in that hydrozoan with a curious inversion of the germ layers that may lay this interpretation open to question.

The functions of the several muscles already enumerated for *Corymorpha* may be studied best by beginning with those of the stalk. When a fully expanded, quiescent *Corymorpha* is vigorously stimulated mechanically, its stalk shortens to about one-half its former length (Torrey, 1904 *b*) and at the same time thickens. Thus an expanded polyp whose stalk measured 4.7 centimeters in length on contraction had a length of only 2.5 centimeters. In ten such instances the average contracted length was 57 per cent. of the average expanded length.

If the hydranth is cut off from *Corymorpha,* the contractility of the stalk remains essentially unaltered. Thus a stalk without hydranth that had an expanded length of 4.2 centimeters had on full contraction a length of 2.3 centimeters and in ten instances of this kind the average contracted length was 55 per cent. of the average expanded length. Thus the contraction and expansion of the stalk are quite independent of the hydranth.

If the activity of the whole stalk is studied, the contraction is seen to occur in only that part which is ordinarily above the mud, the half centimeter or so of buried stalk being incapable of longitudinal contraction. This portion is devoid of longitudinal muscle fibers and hence should be expected to be non-contractile, whereas such fibers are invariably present in that part of the stalk dis-

tal to the buried portion. The contraction of the stalk on its long axis must be attributed, therefore, to the action of its longitudinal muscle.

When the distal end of a decapitated stalk is examined, a plug of large vacuolated cells is seen to protrude from it. These cells, well known to the earlier students of *Corymorpha,* fill the axial part of the polyp and serve to a certain degree as a skeletal tissue. When the polyp contracts longitudinally, they are crowded together lengthwise and on relaxation they doubtless tend to return the stalk to its originally elongated shape. But this operation is probably much facilitated by the action of the circular muscle of the stalk, whose contraction would crowd the mass of axial cells back to its elongated form and thus restore the stalk to its original shape. Thus by the alternate action of the longitudinal muscle and the circular muscle on the mass of axial cells the contraction and elongation of the stalk is accomplished.

If live decapitated stalks of *Corymorpha* are placed in seawater containing magnesium sulphate or chloretone, they soon become incapable of longitudinal contraction. The stalks retain what would be called the elongated condition. If one of these anesthetized stalks, particularly one that has been treated with chloretone, is vigorously prodded at a given spot with a blunt rod, though no longitudinal contraction occurs, in the course of three-quarters of a minute to a minute a constricted ring appears on the stalk and remains there for from five to eight minutes. If the same experiment is tried with a stalk that has not been anesthetized, the stalk immediately contracts lengthwise but elongates soon afterwards, during which a ring of constriction appears and may remain evident for as much as ten minutes.

As the constriction rings produced in these tests must be the result of the contraction of localized parts of the circular muscle and as their formation is quite independent of anesthetization, it follows that the longitudinal and circular muscles must act upon very different principles. The longitudinal muscle contracts much more quickly than the circular muscle does and its activity, unlike that of the circular muscle, is quite abolished by such drugs as chloretone. These features are the characteristics of a muscle under nervous control as contrasted with one brought into action by direct stimulation, and it is, therefore, probable that the longitudinal muscle of the stalk is normally under nervous influence, and that the circular muscle is stimulated directly.

Under such circumstances the interplay between the longitudinal and circular muscles in the shortening and elongation of the stalk as a result of stimulation is easily pictured. Any normal stimulus applied to the stalk gives rise to the impulses that spread through the ectodermic nerve-net and call forth an immediate contraction of the longitudinal muscle. As a result the stalk shortens nearly one-half and the axial cells become crowded together, causing it to thicken proportionally. In consequence of this thickening the circular muscle is stretched, its tonus is probably increased, and it is gradually excited to action, so that on the relaxation of the longitudinal muscle the circular muscle contracts and forces the axial cells back to their original form, thus elongating the stalk. In this way the two muscles are brought into harmonious action though only one of them is under control.

The longitudinal and circular muscles of the proboscis are probably organized upon much the same plan as those of the stalk, but the proboscis is too small an organ

to allow of experimental tests such as have been used with the stalk. Its rapid shortening from a long, narrow organ to an almost spherical one (Torrey, 1904 *b*) and its slow recovery to the elongated form, together with the loss of these activities under chloretone treatment, all point to a condition essentially similar to that of the stalk.

In one respect only is there an observable difference between the musculature of the stalk and that of the proboscis. Occasionally the proboscis exhibits spontaneous peristaltic movements. These begin near the distal end of this organ as ring-like constrictions that progress toward its proximal end. The time required for a single constriction to pass from one end of the proboscis to the other is from half a minute to a minute. Usually not more than one constriction is present on the proboscis at a time. The constrictions are quite obviously due to local contractions in the circular muscle. They must be a very effective means of mixing the contents of the digestive cavity and probably are concerned with driving some of the digestive products of the hydranth downward into the stalk. A similar movement has been known for some time in actinians and has been recently pointed out in *Metridium* (Parker 1916 *a*). Here, as there, it is probably indicative of nervous supervision of a muscle otherwise independent, but on this point no positive evidence has been obtained.

The proximal tentacles in a resting expanded *Corymorpha* radiate more or less horizontally from the basal disc to which they are attached. Each tentacle curves a little downward away from the mouth, but at its free end it turns in the opposite direction and comes eventually to point nearly outward. When stimulated mechanically

such a tentacle shortens a little, perhaps a quarter of its total length, and bends vigorously inward toward the mouth, its free end meanwhile often curling in spiral fashion through one or two turns. The tentacle then gradually relaxes and slowly returns to its original shape and position.

The axis of the tentacle is filled with vacuolated cells not unlike those occurring in the axis of the stalk, and the action of the tentacle can be explained entirely on the assumption that the longitudinal muscle works against the axial cells, whose elasticity returns the tentacle to its original position. In an anesthetized polyp the tentacles are always expanded in what has been assumed to be the resting position and no response can be obtained from them whatever. It is, therefore, probable on physiological grounds at least that there are no circular muscles in the tentacles, but that longitudinal muscles under the control of a nervous system act upon an elastic skeleton of vacuolated cells. The fact that the proximal tentacles on stimulation always bend toward the mouth would lead one to expect that the longitudinal muscle would be more fully developed on the oral than on the aboral side of the tentacle, but of this no direct evidence has been obtained.

The distal tentacles, which are much more incessantly active than the proximal ones (Torrey, 1904 *b*) in moments of rest form a cluster more or less surrounding the mouth. On stimulation they quickly jerk backward away from the mouth and point their tips toward the aboral portion of the hydranth, after which they more slowly return to their original position. On applying an anesthetic, magnesium sulphate of chloretone, to a whole hydranth or to a single isolated distal tentacle, all these reactions disappear in from one to three minutes, to re-

appear after the material has been for about two minutes in pure seawater. It, therefore, seems probable that in the case of the distal tentacles the reactions are dependent upon the same interplay of parts as in the proximal ones, except that the longitudinal muscles of the distal tentacles are probably more fully developed on their aboral than on their oral faces.

No attempt was made to work on the muscles of the peduncles of the medusæ or on those of the medusæ themselves. The peduncles contract on stimulation and the medusæ are more or less rhythmically contractile. Both cease this activity when they are anesthetized with magnesium sulphate or chloretone, and both quickly recover from this condition on being placed in pure seawater. Hence their muscles are presumably under nervous control.

Of the six sets of muscles in *Corymorpha,* the two entodermic muscles, the circular muscle of the stalk, and the circular muscle of the proboscis are both slow in action and uninfluenced by such anesthetics as magnesium sulphate and chloretone. They are, therefore, probably directly stimulated and represent a primitive type of muscle such as is found in sponges (Parker, 1910 *a*) and in certain regions in actinians (Parker, 1916 *a*). Possibly the circular muscle of the proboscis is under certain circumstances somewhat under nervous control as, for instance, when that organ exhibits peristalsis, but ordinarily this muscle, like that of the stalk, probably responds only to direct stimulation.

The four ectodermic muscles, the longitudinal muscles of the stalk, of the proboscis, and of the two sets of tentacles, are relatively quick in action and cease to respond under the influence of anesthetics. These are probably

controlled by a nervous system composed of ectodermic sense-cells and a nerve-net, such as is commonly met with in many cœlenterates (Wolff, 1904; Hadzi, 1909).

Of the effectors of *Corymorpha,* the muscles are the only elements that are under nervous control, a condition that supports the conclusion of Lipin (1911), that in the hydroid *Polypodium* aside from the muscles no other histological elements are dominated by the nervous system.

In attempting to study nervous transmission in *Corymorpha* various stimuli were first tested. *Corymorpha,* like *Tubularia* (Pearse, 1906), is apparently quite uninfluenced by light (Torrey, 1902, 1904 *b*). Though heat and some chemicals are stimulating (Torrey, 1904 *b*), these means of inducing reactions are not so easily controlled as mechanical stimuli. But even here a tremor may be transmitted from the part of the body touched to a distant receptor and thus call forth deceptive responses. For stimulation a faradic current was therefore used. The electrodes for this could be set in place and, after all possibility of accidental mechanical disturbance had passed, the intended stimulus could be applied by simply making the current, thus avoiding any complication from possible tremors. A well localized and controllable stimulus was thus obtained.

If a proximal tentacle of *Corymorpha* is gently touched by a blunt glass rod or stimulated by a very weak faradic current, it will in a second or so after the application of the stimulus bend rather quickly toward the proboscis, after which it will slowly return to its resting position. A more vigorous stimulus will excite to action not only one but many of the proximal tentacles (Torrey, 1904 *b*); the proboscis is also very likely to turn in the

direction of the stimulated tentacle, and the distal tentacles may likewise become active. To a still more vigorous stimulus, not only do the parts of the hydranth respond, but the stalk may contract (Torrey, 1904 *b*). Thus impulses to motion may spread from a single proximal tentacle to any part of the body. The same is true of the proboscis and of the distal tentacles. Conversely, by stimulating the stalk, responses can be called forth from both sets of tentacles (Torrey, 1904 *b*). These observations indicate a diffuse type of transmission, such as is generally assumed for a nerve-net. It is also clear that the stronger the stimulus the more distant the effector that can be activated.

To ascertain something of the nature of the transmission, several kinds of experiments were tried. When a polyp of *Corymorpha* is anesthetized for a few minutes with magnesium sulphate or chloretone, all responses of tentacles, of proboscis, and of stalk disappear except the slow formation of constriction rings in the stalk. The responses thus eliminated may be made to return by placing the polyp for three or four minutes in pure seawater. Since the effectors that are rendered inactive are the ectodermic musculature and since the drugs used are known to act chiefly on nervous tissue, the conclusion is drawn that the essential part of the nervous mechanism of these animals must be in their outer layer, the ectoderm, a conclusion supported by the very short time needed for anesthesia as well as for recovery from this state. It, therefore, seems probable that nervous transmission in *Corymorpha* is an affair of the ectoderm.

To test this view, a polyp about ten centimeters in length was put horizontally in an aquarium and pinned at the middle of its length to a slight elevation of wax so that

its foot-end and its hydranth projected for some distance horizontally and freely into the surrounding water. On applying a faradic current to the hydranth, the foot-end contracted together with the rest of the stalk; on applying it to the foot-end, the hydranth contracted together with the rest of the stalk. The polyp was now unpinned, bent into the shape of a U with the curve where the pin had been and this part was dipped for from one to two seconds into ten per cent. acetic acid and then immediately immersed in pure seawater. As a result of this treatment the ectoderm was killed in a broad ring around the middle of the stalk, but the deeper tissues, at least the axial vacuolated cells, were left alive. On pinning the polyp again in the horizontal position and stimulating it electrically, it was found that the nervous impulse never passed from one end to the other, as in the first trials, but was always limited to the end at which it was applied, showing that the superficial tissue of the polyp, but not its core, is the part concerned with transmission.

This experiment was repeated with the modification that, instead of destroying the superficial tissue with acetic acid, it was anesthetized with chloretone. Polyps thus treated failed to transmit impulses over the anesthetized region, though after ten minutes in pure seawater transmission in this region was reëstablished. As chloretone is known to abolish the neuromuscular activities of the ectoderm, but to leave the entodermic muscles unaffected, it was concluded that the parts concerned with transmission are not only superficial but ectodermic.

To determine whether there are special transmission tracts in the polyp, several lines of experimentation were carried out. A large polyp was split lengthwise from the hydranth end through the column almost to the aboral

end. Such a preparation had the shape of a letter V, with two half hydranths at the free ends of the V and the unsevered base at the angle (Fig. 44). On stimulating one half hydranth with a faradic current both arms of the preparation contracted though the base was outwardly inactive. Hence it was concluded that the base, though without muscle, transmits n e r v o u s impulses from one side of the polyp to the other. If the base is now locally anesthetized and the experiment repeated, the contraction is found to be limited to the arm of the preparation that is stimulated, thus demonstrating the superficial location of the transmitting tissue.

FIG. 44.—A polyp of *Corymorpha* split lengthwise except at its aboral end through which transmission may be accomplished from one arm of the preparation to the other.

Another form of this experiment w a s n e x t tried, in which, however, the two arms of the preparation were united through the hydranth instead of through the base. In this experiment transverse transmission through the hydranth was as easily demonstrated as it had been through the base.

In a third experiment the stalk alone was used, the hydranth and base having been cut off. When one arm of such a preparation was stimulated the other arm almost invariably failed to respond, thus showing that though transverse transmission is easily accomplished in the base or in the hydranth, it is not so easily accom-

plished in the stalk, where longitudinal transmission is the rule.

The predominance in the stalk of longitudinal as compared with diffuse transmission makes localization a significant feature in the responses of this part. If a faradic stimulus is applied to one side of the stalk next the hydranth or next the base, the stalk simply shortens as a whole. If, however, the stimulus is applied on one side of the stalk nearer the middle of its length the stalk bends to that side and usually presses the hydranth with great accuracy against the stimulated spot. This response is not only appropriate for the particular side stimulated but also in most cases for the given level of the stimulated point on that side. The significance of these responses to localized stimulation was often observed in the stock aquarium. This contained by accident a number of small nudibranch gastropods, which were found to feed on the substance of *Corymorpha*. When one attacked a *Corymorpha,* it began near the base of the stalk where the hydroid rose from the mud and as soon as it started to nibble the stalk on a given side the *Corymorpha* responded by applying to the point of attack the hydranth, the tentacles of which were extremely stimulating to the nudibranch and usually drove off the intruder. The success of this form of protective response naturally depended upon the accuracy of the localization.

To ascertain whether transverse transmission is at all significant in the stalk of *Corymorpha,* the following experiment was tried. The stalk of a polyp was cut transversely halfway through at a point midway its length and the polyp was then allowed to come to rest in a vertical position. On stimulating locally below the wound and on the side away from it, the hydranth, as might have been

expected, was applied accurately to the stimulated spot. On applying the stimulus directly below the wound the hydranth was turned to that side but never descended far enough to cover the actual region of the stimulus. The failure here seemed to be due to the deficiency in the musculature as a result of the operation rather than to a defect in transmission. Since a decapitated stalk responds to local stimulation in the type of experiment just described with as much success as a normal one does, it is fair to conclude that, though longitudinal transmission is the predominate feature of the stalk, transverse transmission also occurs in this part of *Corymorpha*.

This conclusion is supported by the observation that a decapitated stalk which has been partly cut through transversely at several different levels and from several different sides, as Torrey (1904 *b*) has already described, will nevertheless localize, though incompletely, a stimulated point.

From the observations and experimental results recorded in this section, it seems fair to conclude that nervous transmission in *Corymorpha* is very probably limited to the ectoderm and is diffuse, except that in the stalk longitudinal transmission predominates much over transverse. Notwithstanding this primitive state of nervous development, reactions that have all the essentials of a nervous reflex may occur. Thus, when a proximal tentacle is vigorously stimulated, not only do it and some of the adjacent tentacles respond, but the proboscis commonly turns toward the point of stimulation. This accurate form of response of a distantly located organ to a circumscribed stimulus has all the characteristics of a reflex, though it is probably dependent upon the activities of a nerve-net that has the capacity of calling into action

more easily those muscles that lie near the receptive position than those that lie far from it.

Enough has already been said to make it quite clear that many of the parts of *Corymorpha* are quite independent of the rest of the polyp in their capacity to respond to stimuli. Thus the stalk of *Corymorpha* will shorten and even localize a stimulus applied to one side of it with as much success after the hydranth has been removed from it as when the polyp is completely intact. There is, therefore, no reason to suppose that the hydranth contains nervous centers that are in any way essential to these responses.

In a similar way the separated hydranth exhibits on stimulation movements in its distal and proximal tentacles and its proboscis that are in all respects counterparts of the movements of these organs in the polyps as a whole, showing that the hydranth is in no sense dependent upon the stalk for its neuromuscular activity. The separate hydranth as well as the separate stalk can be anesthetized with chloretone or magnesium sulphate, and, after having thus lost their responsiveness, these parts will separately recover when placed in pure seawater.

When the proboscis of a *Corymorpha* is cut off, the attached distal tentacles continue to exhibit spontaneous movements and turn vigorously away from the mouth on stimulation as they do on the intact animal, activities that they lose temporarily on anesthetization. The proximal tentacles also exhibit great independence. If one is cut from a hydranth, its curved form brings it to rest on the bottom of a glass vessel on its side and it is comparatively easy to determine by the direction of its curve which is its oral and which its aboral face. On stimulat-

ing it mechanically, it shortens slightly and curls orally, as an attached tentacle does. The same is true when it is stimulated by a faradic current. Under this more favorable method of stimulation a proximal tentacle that had a length of twelve millimeters when at rest shortened to ten on stimulation and curled to a half circle. These reactions disappear after the isolated tentacle has been for five minutes in seawater containing chloretone and reappear on transferring it for three minutes to pure seawater.

If an isolated proximal tentacle is cut in two near the middle, the distal piece coils and the proximal piece curves in response to a faradic stimulus as when they were parts of the whole tentacle. Both parts, moreover, continue to show slight spontaneous movements as the normal tentacle does. All these responses disappear on anesthetization and reappear after the fragments of tentacle have been for a few minutes in pure seawater.

It is quite evident from these observations that the neuromuscular organization of *Corymorpha* is most diffuse and contains nothing that can rightly be looked upon as centralized. In this respect the hydrozoan polyp is, if possible, more a congregation of parts than the anthozoan polyp, which lacks very largely that centralization feature that is so characteristic of the neuromuscular structure and activities of the higher animals.

Among the general activities indicative of the neuromuscular organization of *Corymorpha* none are more important than feeding. If the contents of the digestive spaces in *Corymorpha* are examined, they are found to contain, as Torrey (1904 *b*) has observed, organic detritus composed of the remains of copepods, rotifers, diatoms, and various chlorophyl-bearing protista. The cavity in which these partly digested materials circulate is by no

means simple. Its extent and ramifications can be made out easily by the injection into it of india ink under slight pressure. In this way it can be demonstrated that the body of the hydranth, including the proboscis, contains a considerable digestive cavity (May, 1903). Extensions of this reach out into the peduncles carrying the medusæ, but not into the tentacles. Proximally the digestive space contracts into a central tube as it passes from the hydranth into the stalk, at the distal neck of which it connects with the dozen or more longitudinal canals which extend in somewhat parallel courses proximally through the more peripheral layer of the stalk well down to its buried end. These tubes show not infrequent anastomoses, especially in the proximal portions of their course. The injection of the whole digestive system is best made by cutting off the proximal tip of a polyp, inserting a canula among the vacuolated cells, and after tying it in that position, slowly injecting india ink under slight pressure. The ink quickly makes its way into the canals and flows forward freely till the neck between the stalk and the hydranth is reached. Here commonly a slight block is encountered, due probably in part to the contraction of the sphincter in the circular muscle of the stalk and in part, perhaps, to the fenestrated membrane (Torrey, 1907). By continued slight pressure the ink will suddenly spurt through this neck and quickly fill the cavity of the hydranth, where again it may meet a block if the mouth is closed. This obstruction, which seems also due to a sphincter, may likewise be overcome, whereupon the ink will flow in a fine stream through the mouth into the outer water.

The gathering of food into the digestive cavity is dependent upon one of the best organized and most char-

acteristic sets of responses in *Corymorpha*. In an aquarium through which a gentle current of water has been sweeping and in which the specimens of *Corymorpha* have become well acclimated, they will be found well fixed in the silt, with stalks upright and with their hydranths pointing in the direction in which the current flows. If the current is now shut off, feeding movements will begin in about three to fourth minutes. These have been briefly described by Torrey (1904 *b*) and consist of the following steps. At the beginning of a feeding movement the expanded proximal tentacles with two or three convulsive efforts are drawn together around the proboscis and at the same time the stalk is shortened. The stalk then curves so that the hydranth is brought close to the mud. The proximal tentacles are opened and the distal tentacles and proboscis are applied to the mud. The stalk then slowly straightens and becomes vertical, the proximal tentacles attaining full expansion as the resting position from which the response started is again assumed. The whole response partakes of the nature of a deep bow and requires for its completion about one minute. As a result of it many small bits of detritus and the like become entangled among the distal tentacles, whence they are transferred to the mouth. The proximal tentacles seem to play a very minor part in this type of food gathering. Records on a single individual showed that in one hour twenty feeding movements were made. Of the three minutes involved in each interval, for the intervals were very regular, about one minute was taken up in the actual feeding movement and about two in rest.

When a *Corymorpha* that has been exhibiting a regular sequence of feeding movements in quiet water is subjected to a current of water, these movements cease at

once, to begin again a few minutes after the current has been cut off. Apparently this type of response in normal animals is dependent upon quiet water.

If a *Corymorpha* that is feeding regularly in quiet water is deprived of its hydranth by having it suddenly clipped off at the neck by scissors, the stalk continues the feeding responses but without bowing low enough to bring its distal end close to the substrate. In this sense the response is defective and as the following record shows, it is also slower than before. A normal polyp was found to carry out feeding responses at the following intervals in minutes: 3.5, 3.5, 2.5; whereupon its hydranth was cut off and the stalk continued to respond at intervals in minutes of 5, 4, 5, 4.5, and 5, when the experiment was concluded.

Another curious effect of beheading a polyp was seen in experiments with pairs of feeding individuals. A pair of polyps regularly feeding in quiet water were watched for a short time and then the hydranth of one was cut off; both individuals, the one without a hydranth as well as the one with a hydranth, continued to carry out bowing movements. The circulating current in the aquarium was then turned on, whereat the normal individual ceased to respond while the headless one continued to carry out rhythmic bowing movements. This experiment was often repeated and with uniform results. The water currents in some way stimulate the normal animal so as to cause the feeding responses to cease, a condition that does not obtain in the case of the stalk alone. This response gives more evidence of nervous integration in *Corymorpha* than any other thus far discovered.

After the separation of the hydranth from the stalk, not only does the stalk continue to respond, but the distal

tentacles of the hydranth close and open at regular intervals as they did in the normal feeding responses; the rates of response in the two parts are, however, quite different. Thus in a normal polyp whose feeding movements had been carried out for some time at intervals of 2.5 to 3 minutes the hydranth and stalk were separated, after which the stalk responded every 8 to 9 minutes and the hydranth every 3.5 to 4 minutes. Thus each part individually had a slower rate than the whole animal, the stalk being much slower than the hydranth. It would be natural to expect that one or other of these parts might serve as a pacemaker for the whole system, but of this there is no evidence.

In a similar way a stalk may be cut crosswise in halves and the two halves will continue to show rhythmic contractions. As in the former case, both halves have a slower rate than the whole stalk had. Possibly in both cases the reduced rates give evidence of a general control which is somewhat disturbed by the cutting, though of this there is no conclusive evidence.

Besides the type of feeding that has just been considered and that is apparently characteristic of quiet water, a second type is also to be noted (Torrey, 1904 *b*). When detritus of one kind or another is carried by a gentle current on to the expanded proximal tentacles of an erect *Corymorpha,* these are very likely to wave inward, carrying everything with them toward the distal tentacles, which in turn move quickly outward to meet the incoming proximal members and eventually transport their booty to the mouth. In this way under favorable circumstances much food is doubtless obtained, but the success of this operation is much more dependent upon accident and the whole procedure seems to have less

organized effort about it than the plan of feeding described for quiet water.

The food accumulated by the two methods mentioned in the preceding paragraphs doubtless undergoes digestion in the interior of the polyp and is here moved about by the peristalsis of the proboscis already referred to.

When the responses and activities of *Corymorpha* are compared with those of an anthozoan polyp, their inefficiency is most striking. This is especially well seen in the tentacular responses to food. In an anthozoan the tentacles when touched by a piece of food turn in many directions till they have more or less entwined the food. They become covered with a sticky mucus and they discharge their nettling filaments with great freedom. Finally by the action of their cilia and muscles the food is delivered at the lips. In *Corymorpha* the proximal tentacles are not provided with mucus and their one muscular response is to wave toward the mouth, a response that occurs as well when the food touches their aboral faces, and is consequently left behind by their response, as when it is on their oral face. No cilia are present in *Corymorpha* to help transport the food to the mouth. In *Corymorpha* the whole process of food gathering has a strongly marked mechanical character that makes it much less successful as a means of getting all the food within reach than the operations carried out by the anthozoan tentacle (Torrey, 1904 *b*). This lack of close adjustment, which has been noticed in the tentacles of *Tubularia* (Pearse, 1906) as well as in those of *Corymorpha,* runs through all the reactions of *Corymorpha* as compared with those of the anthozoan polyps.

Notwithstanding the general inefficiency of the responses of *Corymorpha,* this polyp contains among its

muscles about the same array of types as are found in the sea-anemones. Some muscles, like the circular muscle of the stalk, are apparently quite without nervous connections and respond to direct stimulation; others, like the circular muscle of the proboscis, probably respond as a general rule to direct stimulation, though they may be influenced by nervous impulses; and finally muscles, like the longitudinal muscle of the stalk, are completely under nervous domination. Some of these, such as the longitudinal muscle of the proboscis, exhibit responses that are called forth in such a way that they are indistinguishable from a reflex in the higher animals. From this standpoint *Corymorpha* reproduces in miniature all the conditions found in the sea-anemones, and this is further emphasized by the lack of any general nervous center and the consequent great independence of all organs from the side of their neuromuscular activity. *Corymorpha,* therefore, does not seem to fill the gap between the extremely simple effector system of sponges and the receptor-effector systems of the cœlenterates, but rather presents a reduced though not simplified state of the type in the sea-anemone. If the muscles of *Corymorpha* were more commonly open to direct stimulation than they are and if its activities presented less than can be interpreted in the nature of a reflex, it might supply more nearly the requisites of an intermediate type, but, as it is, it resembles rather a reduced actinian than a form in any sense intermediate between sponges and sea-anemones (Parker, 1917 *e*).

SECTION III. CENTRAL NERVOUS ORGANS

CHAPTER XIV

CONCLUSION

It is intended that the present volume shall include an extended discussion of only the simplest examples of the elementary nervous system. In this concluding chapter, however, a brief outline will be given of the relations of this system to the central nervous system of the more complex animals. An outline of this kind must perforce block out only main contours, for, even were they known, it would be impossible in so limited a space as a single chapter to follow the intricacies to be met with in the evolution of that most complicated system of organs, the central nervous system.

It was pointed out in the earlier part of this volume that the neuromuscular system probably did not originate primarily as a nervous structure. The first trace of this system is to be seen in independent effectors, the smooth muscle of the lowest multicellular animals (Fig. 45). This tissue, as seen in the oscular and pore sphincters of sponges, represents muscle unassociated with nerve and acting under direct stimulation from the environment. Such independent effectors are apparently open to only a limited range of stimuli, particularly to those of a physical type, and are relatively slow and sluggish in response. They reappear in the higher animals, as in the acontial muscles of the sea-anemones and in the

heart muscle of the vertebrate embryo, but in the evolution of the neuromuscular mechanism they represent an initial stage and as such they are characteristic of only the simplest forms.

The second step in this series is seen in the receptor-effector system of such animals as the cœlenterates. This step has been accomplished by adding to the independent effector of the lowest forms a receptive element in the nature of a sensory surface. Such receptors arose by the modification of those epithelial cells that were in closest proximity to the already differentiated muscle. These cells, in the form of sensory patches, became espe-

Fig. 45.—Diagram of an independent effector, a muscle cell such as occurs in the lowest multicellular animals.

cially receptive to categories of external changes, such as pressure changes, chemical changes, and changes in heat and light. The disturbances that these changes initiate in the receptive protoplasm are the means by which the subjacent muscles are brought into action. Thus the novel element in this combination, the receptor, serves as a trigger, so to speak, to discharge the underlying muscle, and, judging from the quickness with which this discharge is accomplished as compared with that with which the independent effectors discharge, the efficiency of the new system is beyond doubt.

The receptor-effector system in its simplest conceivable form consists of a patch of sensory cells attached to a group of muscle cells, but practically every instance illustrative of this particular combination is complicated by the fact that the central branches of the receptive cells

are not only applied to the muscle cells but form among themselves a network of communication whereby the impulses that arise from a few receptive cells may be transmitted to many muscle cells instead of being limited to a restricted group. Here is to be seen the first trace of the nerve-net, an organ that in present forms makes the receptor-effector system immensely more responsive and in past forms harbored the germ of a central nervous or adjustor apparatus that in the end profoundly affected the whole scheme of neuromuscular organization.

Fig. 46.—Diagram of a simple type of receptor-effector system such as is seen in the tentacles of sea-anemones. It consists of receptors *r* or sense cells whose basal nerve-net connects them with the deep-seated muscle cells *m*.

The simplest type of receptor-effector system with a simple form of nerve-net is such as is seen in the tentacles of many actinians where the receptive cells with their central branches and the muscle cells constitute the whole complex (Fig. 46). A more complicated type of this system and one that is more usual with the cœlenterates is that in which, in addition to the two kinds of cells mentioned, a third appears and from its position in the midst of the nerve-net adds by its numerous branches immensely to the intricacies of this structure (Fig. 47). This third type of cell was long ago recognized by the Hertwigs (1879–1880), who designated it a ganglion cell and attributed to it central functions such as were formerly supposed to be of necessity associated with such elements. Cells of this kind, according to Havet (1901), intervened between the sensory cells and the muscles, and he, therefore, denominated them motor cells. As they are not massed together into ganglia and as they may

have other functions than the control of muscles, it appears that neither of these names is especially appropriate. They are the cells in the simpler types of nervous system from which the neurones of the more complex types have been derived. Hence the name protoneurone, as already suggested, is not inappropriate (Parker, 1918 *a*). A receptor-effector system whose nerve-net includes protoneurones is, therefore, a step nearer a centralized nervous system of the higher animals than one in which the protoneurone is not present.

FIG. 47.—Diagram of a complex type of receptor-effector system such as is seen in many parts of sea-anemones. It consists not only of receptors *r*, with their nerve-nets, and of muscle cells *m*, but also of the so-called ganglion cells *g* in the nerve-net.

Although a receptor-effector system may consist of highly differentiated s e n s e organs connected by a protoneurone nerve-net with distantly located muscles, it nevertheless is very far from representing even a simple central nervous system. First of all, such a receptor-effector system exhibits in a marked degree a state of diffuseness. The animals possessing such systems have no single nervous organ to which their nervous experience may be said to be referred and from which their impulses to response emanate. Their nervous activities are uncentralized. Each important organ, like the tentacle or the foot of an actinian or the column of *Corymorpha*, has within itself its own neuromuscular organization, and the autonomy thus conferred on this part is one of the characteristics of the effector-receptor system.

This system is further characterized by great diffuseness of transmission. Any nervous impulse started up

in it at any point is very likely to spread wave-like throughout its whole extent. This form of diffuse transmission is in strong contrast with that kind of transmission that is carried out in the nervous systems of the higher animals where impulses follow definite paths inward and outward, reaching finally only special groups of muscles or even single muscles. These two features,

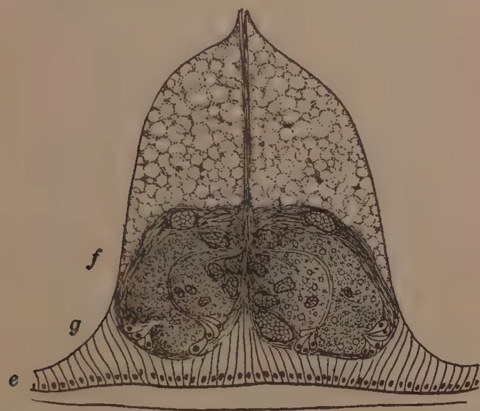


FIG. 48.—Transverse section of the ventral nerve-chain of the marine worm *Sigalion* showing this chain as a thickened portion of the superficial ectoderm in which the sequence of tissues from the exterior inward is superficial epithelium *e*, ganglion cells *g*, and nerve fibers *f*. (After Hatschek, 1888.)

the absence of a central station and the diffuseness of transmission, both of which are aspects of the same general condition, are the most striking characteristics of the receptor-effector system and bring this system into strong contrast with that final type of neuromuscular organization that is characteristic of the highest animals and in which a central nervous organ or adjustor is well differentiated.

This most highly differentiated type of neuromuscular system in which an adjustor or central organ has arisen

between receptors and effectors represents the final step in the growth of this group of organs. As just indicated, the novel element in this particular combination is the central organ or adjustor, and this arises in the region between the receptor and the effector and out of that material which in the elementary system constitutes the nerve-net. Its growth is associated with an inward migration whereby it retreats from the surface of the animal to a deeper situation and comes thus to gain what is significant of its growing importance, a certain degree of protection. In the cœlenterates the nervous elements are mostly contained in the epithelial layers of the body and especially in the external epithelium, the ectoderm. In the worms, where the body has gained greatly in thickness and solidity as compared with the cœlenterates, this inward migration is clearly seen. These animals no longer possess the diffuse system of the lower forms, but have a definitely centralized band of tissue extending the length of the body. The relation of this band to the ectoderm is well seen in a series of annelids. In *Sigalion,* a marine worm, this band, which consists of a brain and a ventral nerve-chain, is still a part of the superficial ectoderm (Fig. 48). In *Nereis,* by a process of delamination, the ventral chain has freed itself from the skin, though the brain is still a part of that layer. In the earthworm this process has been carried to its completion and the whole nervous band has separated from the ectoderm and migrated into the deeper parts of the animal (Fig. 49). This condition of a deep-seated central nervous organ is characteristic of the higher invertebrates such as the arthropods, mollusks, and so forth, and, as their embryology shows, it was brought about by a process analogous to that seen in the worms. In the vertebrates this inward

migration of the central organ also takes place, but in this group it is accomplished, not by a process of delamination, but by an involution of a portion of the skin itself. The infolded layer of ectoderm thus produced assumes the form of a tube and the walls of this tube by differentiation give rise to the spinal cord and brain, the two chief organs in the central nervous system of these animals.

The concentration of the diffuse nervous activities of the lower animals from the skin in general to a par-

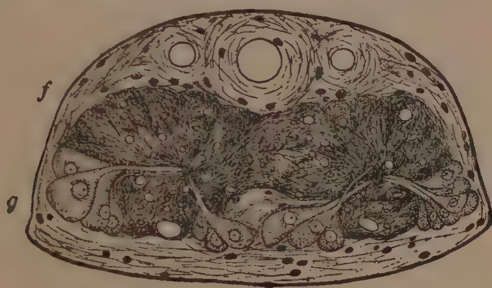


FIG. 49.—Transverse section of the ventral nerve-chain of the earthworm *Allolobophora* showing this chain as separated from the superficial ectoderm of the worm but still retaining on its ventral or more superficial side the ganglion cells *g*, and on its deeper side the nerve fibers *f*. (After Hatschek, 1888.)

ticular part of this layer and the separation of this part from the rest of the skin, together with its migration into a deeper position in the animal, are rearrangements in which are retained a good deal of the original distribution of the elements as seen in the more primitive systems. Thus in the cœlenterates the elements of the receptor-effector system consist of cell-bodies in the superficial part of the epithelium, followed by transmitting fibers in the midregion, and finally completed by muscle fibers in the deepest part (Fig. 3). When this system concentrates and breaks away from the skin, as it does in the annelids and the higher invertebrates, it is not sur-

prising to find that the muscle occupies much of the interior of the body and that in the nerve chains the cell bodies are on the side next the skin and the transmitting trunks on that away from this layer (Fig. 49). The same sequence occurs in the vertebrates except that in this instance the epithelial layer of the skin instead of being left on the exterior of the animal is infolded and lines the central canal of the nervous system whose surface is derived from the exterior of the animal. Proceeding from this surface (Fig. 50) with its epithelial covering toward the other surface of the spinal cord the grey matter or region of the ganglion cells and fibrillar material is first passed through and then the white matter, the region of nerve fibers where transmission is the chief function. Thus the sequence of tissues established in the receptor-effector systems of cœlenterates impresses itself on the differentiated central organs of the higher invertebrates and even the vertebrates.

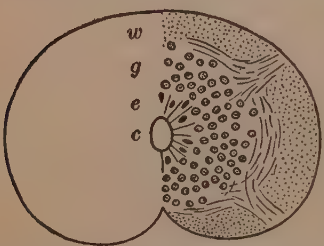


FIG. 50.—Diagram of a transverse section of the spinal cord of a vertebrate (salamander); *c*, central canal; *e*, epithelium; *g*, grey substance composed of ganglion cells and fibrillar material; *w*, white substance or nerve fibers.

When an attempt is made to follow out the differentiation of the nervous elements in the evolving central nervous organ, it is necessary to begin with some of the processes that show themselves first in the nerve-net. As already pointed out, the nerve-net in its most typical condition exhibits diffuse nervous transmission and in this respect is in strong contrast with the central nervous organs of the higher animals whose transmission capacities are highly specialized and limited. A kind of polar-

ity that is indicative of this specialized state is well known to occur, however, in certain nerve-nets. For instance, it has been pointed out that in the tentacles of sea-anemones transmission is much more freely accomplished in a proximal direction than in a distal one. This was shown to result from the direction taken by the nerve-fibrils in the nerve-net of the tentacles. Probably a similar aggregation and alignment of fibers of the net into definite tracts is responsible for the simple reflex by which a stimulation of the tentacles of a sea-anemone by food will cause its transverse mesenteric muscles to contract and thus open its œsophagus. In some such way as this a diffuse nerve-net may be pictured as converted into the beginnings of a central nervous organ in that its network of transmitting fibers can be supposed to be rearranged into systems of tracts whose connections are such that transmission becomes at once limited and specialized.

But such a polarized derivative of a nerve-net is probably still far from even a simple central nervous organ. Such a polarized nerve-net is to be met with in the myenteric plexus of the vertebrate intestine, but the remoteness of this structure from a central organ is well understood when we compare its activities with those of the vertebrate brain. The polarized nerve-net transmits in either direction. Its chain of protoneurones carry impulses up or down the series with indifference. This is in strong contrast with the state of these cells when they have arrived at the condition of neurones. It has long been known that in the spinal cord of vertebrates impulses may be sent over dorsal neurones into the cord to reappear in ventral neurones and excite muscle contraction, but that it is impossible by stimulating ventral neu-

rones to excite the corresponding dorsal elements. The course that is open to transmission in one direction is not open in the opposite direction. This state occurs apparently wherever one neurone joins another and, as it is known not to be characteristic of transmission within a single neurone, it is assumed to be peculiar to the region in which the impulse is transmitted from one neurone to another. The special mechanism resident in this situation and valve-like in its action is known as the synapse. It limits polarization in that it allows nervous transmission to occur only in one of the two possible directions. It is perhaps the most general and definite criterion of a central nervous organ. It would be an extremely important step if an easy test for the presence of synapses could be established. Anatomically this is probably quite impossible because of the very minute size of the structures concerned. Physiologically it might be attained, and already an interesting suggestion in this direction has been made by Moore (1917). It has long been known that strychnine greatly heightens the reflex excitability of many animals and it has been commonly assumed that this action is due to the reduction, under the influence of this drug, of the synaptic resistances. Hence strychnine and other drugs having related effects may be used as a test for the presence of synapses. From this standpoint Moore's results are of extreme interest, for he has found that the drug has no effect on the neuromuscular responses of cœlenterates, a slight one on echinoderms, a much greater one on crustaceans and mollusks, a series that leads up to the well-known condition in vertebrates and suggests in its continuity that the effects are dependent upon the appearance and degrees of differentiation of the synapse.

The conversion, therefore, of a system of protoneurones without synaptic interruptions into one of neurones related through synapses is the essential step in passing from a nerve-net to its derivatives, a true central nervous organ. In animals in which nerve-nets prevail, the lower invertebrates, the embryonic cells that give rise to their protoneurones are in the course of their development near neighbors so that the intimate relations which they bear to one another in the final net may after all be an expression of that closeness of relation that has existed between them from their embryonic states onward. It is not impossible that protoneurones that are united with each other in the nerve-net retain their strands of connection from embryonic stages when in the course of cell division they were never really entirely separated.

With the neurones of the differentiated central nervous system the case is usually very different. In the embryo of one of the higher animals the neurones are represented by cells without processes, the neuroblasts, which, as they differentiate into neurones, do so in part by the production of extensive processes. In this way two neuroblasts that lie at almost the opposite ends of the developing nervous system may by means of their processes connect directly with each other as neurones in the adult. Thus certain neuroblasts in the developing cerebral cortex of mammals differentiate into neurones by throwing out processes that eventually reach in a remote part of the spinal cord motor neurones whose neuroblasts could have had no possible connections with those in the cortex. Both sets of cells are in the beginning widely separated and their final union depends upon the cell processes that have grown from one set to the other. How intimate this

union is, is not known, but that it is not a union of the kind seen in the nerve-net is quite clear. As was indicated in the discussion of synaptic transmission, the union is not complete, for it transmits in only one of the two possible directions. In picturing the conversion of a nerve-net into a central nervous organ, the longer and longer stretches over which nervous connections must be established as the higher and larger animals have been evolved must be kept in mind as a process which, as met with in embryonic life, implies a growing together of dis-

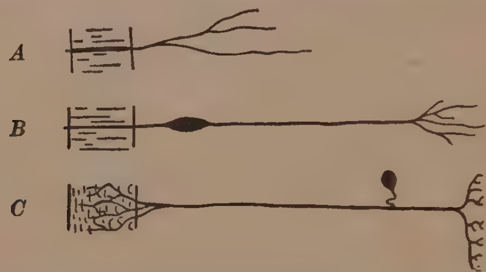


Fig. 51.—Stages in the differentiation of sense cells; *A*, sensory protoneurone from a cœlenterate; *B*, sensory neurone from a mollusk; *C*, primary sensory neurone from a vertebrate. In each instance the peripheral end of the cell is toward the left, the central toward the right.

tantly located cells, a process that thus gives ample opportunity for the establishment of such relations as are seen in the synapse and which, therefore, has been of fundamental importance in the evolution of the highest form of nervous system.

The types of cells that the synaptic nervous system has received from the nerve-net are easily designated. The most primitive nerve cell from the standpoint of animal phylogeny is the sense-cell, or receptive cell, such as occurs in the sensory epithelium of the cœlenterates (Fig. 51, *A*). In this type of cell, the cell body with its nucleus lies in the epithelial portion of the skin of such animals.

This sensory protoneurone, for such it may be called, has been inherited by the higher invertebrates in an unmodified form except that in some, as the mollusks for instance, its cell body shifts from a position in the superficial epithelium into a deeper or subdermal one (Fig. 51, *B*). Finally in the vertebrates the cell body comes to occupy a still deeper position as the whole element assumes the form of a primary sensory neurone in that group (Fig. 51, *C*).

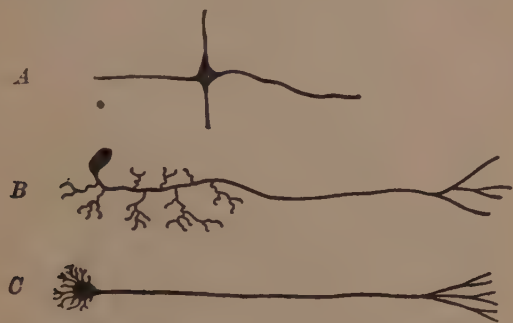


FIG. 52.—Stages in the differentiation of nerve cells; *A*, protoneurone from the nerve-net of a cœlenterate; *B*, motor neurone of an earthworm; *C*, primary motor neurone of a vertebrate. In *B* and *C* the receptive end of the neurone is toward the left, the discharging end toward the right.

The protoneurones of the nerve-net, the second type of nervous element to be differentiated, give rise to the remaining neurones of the synaptic system. The general change that they undergo is relatively simple. As protoneurones in the cœlenterate nerve-net, their cell bodies usually possess a central position in relation to the radiating system of nervous processes to which they give rise (Fig. 52, *A*). With the introduction of polarity and the synaptic relations, the cell body migrates toward the receptive end of the cell (Fig. 52, *B*), at which it is commonly located in the fully differentiated neurone (Fig. 52, *C*). Neurones of this type fall under one or other of

two classes, primary motor neurones or internuncial neurones. The primary motor neurones, the more primitive of the two, extend from the central organ to a muscle some of whose fibers they control. The internuncial neurones connect one part of the central apparatus with another and their courses, therefore, are entirely within the limits of the central organ. The more primitive central nervous organs such as those in the worms consist of little more than primary sensory and motor neurones. These of themselves constitute a sufficient basis for the simple types of reflex. But besides these there are a few internuncial neurones for internal connections. Above the worms in such forms as the arthropods and mollusks, the internuncial neurones become proportionally more abundant than the other types of neurones and in the vertebrates the internuncial type composes the chief mass of the central organs, a feature that reflects the enormous development of associative operations carried out by the vertebrate as compared with the invertebrate.

But the nervous system of the higher animals is not only a system of tissues derived from a small group of especially sensitive cells associated with a still more primitive element, the musculature. It is a system that in its more differentiated examples has appropriated to itself certain other elements of the body than those that can be looked upon as direct descendants from an original source. In the vertebrates, at least, the primary sensory neurones have in some instances, as in the ear and in the organs of taste, appropriated ectodermic cells from the ordinary integument, and these cells, as taste buds and auditory hair cells, have come to form a constituent part of the sensory mechanism. Without doubt these appropriated cells add to the effectiveness of the apparatus

concerned. Thus the free-nerve terminations concerned with touch in the vertebrate skin require a much more vigorous mechanical stimulus than do the auditory hair cells in the ear, cells that have been appropriated by just such a system as that seen in the tactile terminations. The same is true of the chemical senses. The free terminations of the primary sensory neurones of the human mouth (Fig. 53, *A*) are sensitive to solutions of ethyl alcohol not less in concentration than 5 molecular, whereas those connected with taste buds (Fig. 53, *B*) are stimu-

A

B

FIG. 53.—The appropriation of secondary sensory cells by primary sensory neurones in the vertebrates; *A*, primary sensory neurone associated with the mouth surface of a vertebrate and concerned with the common chemical sense of that surface; *B*, a primary sensory neurone that has appropriated secondary sensory cells as represented by those in a taste bud in the vertebrate mouth. In each example the peripheral end of the neurone is toward the left, the central toward the right.

lated by a solution of concentration 3 molecular (Parker and Stabler, 1913). Hence wherever a primary sensory neurone has appropriated secondary sensory cells, there is apparently an increase in the sensitiveness of the resulting combination.

Not only have the sensory or afferent neurones of the differentiated nervous system appropriated cells not originally a part of the system, but the efferent neurones have also associated themselves with effectors not in the beginning under nervous control. Just as muscle arose as an independent effector, so other like elements have made their appearance in the animal series. To these categories belong cilia, nettle cells, chromatophores, luminous organs, glands, and so forth. Electric organs

are probably not of this nature, for in all cases they appear to be modified muscles rather than independently produced structures. The others, however, give every evidence of independent origin and still exist in many animals as structures unassociated with nerves. Cilia proper and nettle cells seem never to have come under nervous domination, but chromatophores, luminous organs, and glands have all in one instance or another been appropriated by the nervous system. Through this agency they have been more or less completely removed from the class of organs whose action is called forth by direct stimulation and have been made subservient to the nervous system. Thus the system that arose secondarily around an independent effector muscle, has in the end gained such supremacy as to take to itself a number of independent effectors, any one of which might in the beginning have served as the nucleus around which the first nervous tissue could have taken origin.

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